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Journal of the Fisheries Research Board of Canada

Journal de l'Office des recherches sur les pêcheries du Canada

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Editorial

The name of the *Journal* will change to the *Canadian Journal of Fisheries and Aquatic Sciences* beginning with the January 1980 issue. I regret any inconvenience this change may cause and would like to explain briefly why such a decision was made.

Recently, a Bill was passed by the Federal Government which repealed the Fisheries Research Board (FRB) Act and all elements of the FRB were incorporated into the Department of Fisheries and Oceans. Because the FRB no longer existed, it was decided that a new title was necessary.

The *Journal* received its international reputation under the auspices of the FRB and particularly under the stewardship of our dearly loved and respected Editor Cam Stevenson whose recent death caused great sorrow to all of us here and to his many colleagues worldwide. The Science Citation Index® shows that the *Journal* is one of the most highly cited aquatic science journals. Thus it has been difficult for us to consider a name change. Moreover, we are keenly aware of the problems a name change causes for all elements of the scientific information transfer system, particularly computerized searching which is fast becoming the prime method for current awareness and retrospective searching of the literature.

Choice of the new title was not easy. The final outcome will not suit everyone but it has advantages over the previous titles in being free of ties to the sponsoring organization and more descriptive of the *Journal*'s scope. I anticipate that the new title will survive for the life of the *Journal*, and this should encourage its acceptance.

It is not my intention to change the *Journal*'s general editorial policy which is to encourage publication of the best manuscripts in fisheries and aquatic sciences. To do this we will continue to provide first class service in scientific editing, peer review, and publication production.

I do, however, want to encourage all fisheries and aquatic scientists to provide constructive criticism of the *Journal*. Only with such support and involvement can we be relevant to particular needs and continue to communicate top quality scientific information to as broad an audience as possible.

J. WATSON
Acting Editor and Director of Scientific Information

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Éditorial

A compter de janvier 1980, le *Journal* changera de nom et s'appellera *Journal canadien des sciences halieutiques et aquatiques*. Ce changement causera des inconvénients que je regrette. Je voudrais donc vous exposer brièvement les raisons d'une telle décision.

Le gouvernement fédéral adoptait récemment un bill annulant la Loi sur le Conseil de recherches sur les pêcheries (Office des recherches sur les pêcheries, ORP) et tous les éléments de l'ORP furent incorporés au ministère des Pêches et des Océans. L'ORP n'étant plus, il fallait un titre nouveau.

C'est sous les auspices de l'ORP que le *Journal* se mérita une réputation internationale, plus particulièrement sous la direction de Cam Stevenson, aimé et respecté de nous tous, et dont la mort récente fut pour nous et de nombreux collègues de la communauté internationale une source de profonde tristesse. Selon le *Science Citation Index*®, le *Journal* est un des périodiques en sciences aquatiques le plus fréquemment cités. Il fut donc assez difficile de considérer un changement de nom. En outre, nous sommes bien au fait des problèmes qu'un changement de nom soulève auprès de tous les éléments du système de transfert d'information scientifique, en particulier la recherche documentaire mécanisée, qui devient rapidement la principale méthode de recherche, tant courante que rétrospective.

Le choix du nouveau titre n'a pas été facile. Bien sûr, il ne plaira pas à tous mais, contrairement à l'ancien titre, il n'est lié à l'organisme dont il dépend et représente mieux la portée du *Journal*. Le nouveau titre, j'ose croire, durera la vie du *Journal*, ce qui devrait encourager son acceptation.

Le *Journal* a comme politique d'encourager la publication de travaux de haut calibre en sciences halieutiques et aquatiques, et ce n'est pas mon intention de la modifier. Dans ce but, nous continuerons d'offrir un service de rédaction scientifique, de critique par les paires et de production de premier ordre.

Je voudrais toutefois encourager tous les spécialistes des sciences halieutiques et aquatiques à critiquer de façon constructive le *Journal*. Ce n'est qu'avec un tel appui et participation que nous pourrons satisfaire à des besoins particuliers et continuer de transmettre une information scientifique de haute qualité à un auditoire aussi varié que possible.

J. WATSON
Rédacteur et directeur intérimaire
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Influence of Benthos Life History upon the Estimation of Secondary Production[1]

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WATERS, T. F. 1979. Influence of benthos life history upon the estimation of secondary production. J. Fish. Res. Board Can. 36: 1425–1430.

Synchrony of cohorts is one of the life history features having most important effects upon the estimation of benthic secondary production, because most methods depend heavily upon recognition of discrete cohorts. The Hynes method, intended to circumvent the necessity of cohort distinction, still depends upon determination of trophic level, voltinism, minimum and maximum sizes, and length of aquatic life. Knowledge of preferred habitat, distribution, and behavior are essential for accurate production estimates. Use of the production:mean standing stock (P/B) ratio (fairly constant at about 5 for cohort P/B of benthic invertebrates) to approximate production from standing stock data, also must account for trophic level, voltinism, and length of aquatic life. Various life history features are compared as to their probable effect on production estimation; in addition, they are compared to the effect of sampling errors.

Key words: benthos, life history, production, secondary production, productivity

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Parmi les caractéristiques du cycle biologique affectant le plus l'estimation de la production secondaire benthique, il y a la synchronie des cohortes, car la plupart des méthodes dépendent étroitement de la reconnaissance de cohortes distinctes. La méthode de Hynes, visant à contourner la nécessité de distinguer les cohortes, dépend toujours de la détermination du niveau trophique, voltinisme, tailles minimales et maximales et durée de vie aquatique. On ne peut en arriver à des estimations précises de production sans connaître l'habitat préféré, la distribution et le comportement. Niveau trophique, voltinisme et durée de vie aquatique doivent également ressortir du rapport production: biomasse moyenne (P/B) (se maintenant assez uniformément à environ 5 parmi les cohortes d'invertébrés benthiques). Nous comparons diverses caractéristiques du cycle biologique quant à leur effet probable sur les estimations de production et, en outre, sur les erreurs d'échantillonnage.

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THE recent symposium on benthic life histories, held at the 1978 meetings of the North American Benthological Society, the proceedings of which were published by this journal (Rosenberg 1979), involved many aspects of benthic science affected by life history features. Included were technical procedures of sampling, taxonomy, and bioassay, which can be influenced by life history data; in addition, it was demonstrated that certain life history features such as developmental rate and voltinism can themselves be influenced by environmental factors such as temperature and the organisms' diet. One topic that was touched upon briefly was the influence that life history may have upon the estimation of secondary production (Resh 1979). Secondary production is defined here as the rate of tissue elaboration by a population of heterotrophic organisms. In benthic science, various aquatic macroinvertebrates usually comprise these populations — insects, crustaceans, molluscs, etc. — at both the herbivore–detritivore and carnivore trophic levels. Secondary production is usually expressed in terms of biomass produced per spatial unit per unit time — e.g. $kg \cdot ha^{-1} \cdot yr^{-1}$, $g \cdot m^{-2} \cdot d^{-1}$; or biomass units may be converted to energy units, usually calories or Joules, with which production at various trophic levels may be more meaningfully compared. The estimation of secondary production from field data is accomplished by procedures that depend necessarily upon various life history features of the species involved; in fact, it has been the lack of life history information, or life histories so complex that critical information cannot be determined from field samples, that has slowed the accumulation of production data in the past.

Thus the purpose of this paper is to explore more thoroughly the relationship between certain life history features and production estimation, to point out some of the major gaps in our present state of life history

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knowledge, and to suggest the direction of future life history research that would lead toward an improved methodology in secondary production.

Secondary Production — Methods of Estimation

Cohort-Based Methods

The history of method development in secondary production has ranged largely around the aspect of synchrony of cohorts or generations and the problem of recognizing an individual cohort (see Waters 1977 review of secondary production for discussion of methods). The very earliest attempts at estimating production involved summing up the losses that occurred progressively from a known cohort, considering that the total losses from a cohort equaled the total production of that cohort (Boysen-Jensen 1919). Other attempts that followed, using such "removal-summation" methods (e.g. Borutsky 1939; Anderson and Hooper 1956), or the similar techniques of "increment-summation" (Pechen and Shushkina 1964; Kajak and Rybak 1966), also involved data collected from known cohorts. The method introduced by Ricker (1946) and Allen (1949) involved the computation of production as the mathematical product of mean standing stock and instantaneous growth rate; it has long been assumed that growth data could be obtained only by periodically sampling and measuring the increase in mean individual weight of a recognizable cohort, although fundamentally the method requires only that growth data be acquired by any valid means. Ricker and Allen's method was later modified by Allen (1951) in that it involved a planimetric determination of area under a density–mean weight curve, but again for a known cohort. Their methods were developed first for fish populations in which, through the scale method, it was fairly easy to recognize a cohort, or year-class in the fisheries usage. The "physiological" method and early methods used for zooplankton with continuous reproduction (discussed in Waters 1977 review) did not rely upon distinction of cohorts, but these methods require laboratory culture for data that must be extrapolated to field populations, a procedure with considerable risk.

Thus, it was felt for a long time that reliable production estimates could be made only for recognizable cohorts or year-classes. A severe limitation upon production research was obvious with invertebrate populations, because the life histories of invertebrates are so varied, or unknown, as to make the recognition of cohorts possible for only relatively few species.

The Hynes Method

The method more recently proposed and developed by Hynes (1961), Hynes and Coleman (1968), and Hamilton (1969) was a marked departure from earlier techniques in that it did not depend strictly upon application to a recognizable cohort, nor even to a single species. But rather it was based upon the calculation of an "average cohort," or the mean size distribution of animals collected over a year, and production is estimated basically as the sum of losses between size-classes. The original intention of the method was that it apply to the entire benthic fauna, or at least to a group of species, and no claim for a precision beyond an order of magnitude was made. Nevertheless, the method has now been tested many times with empirical data on single species populations and compared with the earlier methods; invariably, the Hynes method results have compared well with the results of the other methods (e.g. Hudson and Swanson 1972; Neveu 1973, 1977; Waters and Crawford 1973; Cushman et al. 1975; and others), and the method appears now to be well accepted as valid in its basic procedure, with potential errors not nearly as large as an order of magnitude.

Various limitations arise, however, when the Hynes method is applied to more than one species, and these all appear related to various life history features of the benthic invertebrates involved. First it is necessary that the species in a benthic fauna be separated by trophic level. Viewing production in terms of energy flow rates, production rates of herbivore–detritivores and carnivores are not additive, since the production of the latter is actually part of the production of the former. A combined estimate in terms of biomass would express a correct total of that produced. But since a part (carnivores) is the result of eating another part (herbivore–detritivores), such an estimate would be an overestimate of the biomass made available to the rest of the community. Second, only those species of the same voltinism may be treated as a group. Third, several species may be treated together only if their minimum and maximum sizes are approximately the same; a mix of species capable of growing to different sizes will result in an overestimate. Even within the same species, if the two sexes attain different maximum sizes, some overestimate will result (Waters and Crawford 1973).

Thus, it appears that an entire benthic fauna should not be treated as a group (or at least rarely), and that the Hynes method for maximum accuracy must be applied to various subgroups according to such life history features as trophic level, voltinism, and sizes attainable.

Another life history feature that has recently been recognized as critical to the accuracy of the Hynes method is the proportion of generation time that the species is available in its habitat for sampling (Benke 1979). If this proportion is substantial, it will cause a serious underestimate. For example, if a univoltine insect species is available for sampling for only 9 mo of the year (3 mo in egg, pupa, or adult stage), the annual production as computed by the Hynes method should be corrected by multiplying by 12/9. Benke refers to this length of aquatic life, during which the species is present and growing, as the cohort production interval (CPI) in days, and the estimate is corrected by multiplying be 365/CPI. This procedure automatically takes into account the correction for multivoltine or semivoltine species, instead of multiplying by the number or fraction of cohorts per year, as Hamilton (1969) indicated. Clearly, this refinement complicates the application of the Hynes method; it would be most important where the CPI is short in relation to the full generation time and probably will not significantly affect estimates made on many benthic invertebrates. However, many species of insects at least do have a very short CPI, e.g. the mayfly *Tricorythodes atratus* (Hall et al. 1980) and many chironomids and black flies.

P/B Ratio

Considerable data have now been accumulated on the P/B, or turnover, ratio, which is the ratio of production to mean standing stock. The P/B ratio must be specified as a cohort ratio or an annual ratio; the former is easier to obtain, whereas the latter is more useful in its application to estimate production from standing stock data. The cohort P/B ratio appears to be fairly constant, at least within a

group with similar life history, and for benthic invertebrates it appears to be about 5 (Waters 1977). Thus, the annual P/B ratio for a univoltine species will be about the same or somewhat higher (see below), twice as high for bivoltine species, etc.

To estimate annual production from mean standing stock and a P/B ratio, species must be grouped at least by trophic level and voltinism, and then mean standing stocks are multiplied by appropriate annual P/B ratios. This may seem an imprecise estimate of production (but see Relative Quantification section below), although the results may be satisfactory in natural resources management applications, such as fisheries and pollution control evaluation. The trout stream manager, for example might profitably revive the old "forage ratio" method of determining fish stocking rates with such benthic production estimates instead of standing stock data. However, he would need to know the trophic level and voltinism for the principal benthic species utilized as food by the fish, life history information that is all too often lacking.

The determination of the correct annual P/B ratio may not be simply a matter of multiplying the number of generations per year by 5. If a substantial proportion of the year is spent in an unavailable form (egg, etc.), then the annual P/B ratio will be higher (Waters 1969). The effect of the CPI is similar to that in the Hynes method, as pointed out by Benke (1979). For example, the bivoltine *Tricorythodes atratus* (Hall et al. 1980) spends a large portion of the year in the egg stage, and the annual P/B ratio, instead of about 10 as might be expected from its voltinism, was much higher at 26.

Critical Life History Features

Voltinism

It appears clear that voltinism and length of aquatic life (CPI) are two of the most important life history features influencing secondary production estimation. Fortunately, a number of recently published reference texts include much good summary information on voltinism for the major benthic groups: Plecoptera (Hynes 1976), Ephemeroptera (Edmunds et al. 1976), Trichoptera (Wiggins 1977), aquatic insects (Merritt and Cummins 1978), and freshwater invertebrates (Pennak 1978). For the most part, the voltinism is given generally for families and sometimes to genus, but rarely to species; however, general knowledge of voltinism for a family or genus may not be sufficient, since variation does occur within a family or genus. Even within a known species, voltinism may vary depending on water temperature, especially for Ephemeroptera (Edmunds et al. 1976) and Trichoptera (Mackay 1979).

Most trichopterans are apparently univoltine, but multi-voltinism does occur (Wiggins 1977; see review of Mackay and Wiggins 1979). And new evidence increasingly indicates more than one generation per year, particularly in warmer waters (Rhame and Stewart 1976; Mackay 1979; A. C. Benke, School of Biology, Georgia Institute of Technology, Atlanta, GA 30332, USA, personal communication). The Hydropsychidae, especially *Hydropshyche* and *Cheumatopsyche*, constitute some of the most common invertebrates in streams, are frequently in great abundance, comprise an important proportion of stream fish diet, and must constitute a substantial part of many streams' energy budgets. Yet few production data appear in the literature for the hydropsychids, presumably because of the difficulty in distinguishing coexisting species in early instars and thus their voltinism; recent work, however, has resulted in progress in this aspect (Mackay 1978, 1979; Benke and Wallace 1979), and production data appears forthcoming (Benke and Wallace 1979; M. B. Macfarlane unpublished data; Parker and Voshell 1979; R. J. Mackay, Biology Department, McGill University, Montreal, Qué., Canada, personal communication).

For Ephemeroptera, voltinism is more variable, different species being uni-, bi-, or even trivoltine, as well as semivoltine (Edmunds et al. 1976). Since the CPI and voltinism may vary within a species dependent on water temperature, the determination of a species into a mode of voltinism in one locality does not necessarily mean the same species will exhibit the same voltinism elsewhere. And because some stream mayflies frequently exhibit extremely high invertebrate drift, it is entirely possible that such a population may, part way through its life cycle, drift from an area conducive to two generations per year to an area downstream that is conducive to three generations per year, a formidable problem for the production researcher indeed. Some members of the Ephemeroptera are extremely difficult to distinguish as immatures. Early instars in the genus *Baetis*, one of the most common in many streams, are particularly difficult, although major advances in identification in this group have been made recently (Bergman and Hilsenhoff 1978).

The Plecoptera and Diptera (particularly chironomids and black flies), two other major aquatic insect groups, also have important voltinism aspects in production estimation. The Plecoptera are probably the most important among those invertebrates with life cycles longer than one year, although many are univoltine, while bivoltinism is doubtful (see review of Hynes 1976). The length of time for egg incubation is variable, with sometimes a large portion of the year required; correspondingly, the CPI will vary among stonefly species, affecting production estimation. The stoneflies also include many carnivorous species. Chironomids and black flies frequently constitute the majority in numbers in benthic faunas; both groups may include multivoltine populations and very short CPIs. Consequently, it may be expected that their production is often greatly underestimated. Voltinism is highly variable in the Chironomidae, ranging from many generations per year to life cycles of several years in duration, temperature being the main responsible factor (Oliver 1971; Butler 1979). The many generations per year, short CPIs, and consequent overlapping cohorts present in field samples may make distinction of cohorts impossible, and therefore laboratory culture may be necessary for production estimation (Mackey 1977).

Both the Hynes method and use of the P/B ratio require knowledge of the CPI. Estimating this factor undoubtedly is more difficult than determination of voltinism, but unless it is known to be so little different from a full year (for univoltine species, or one-half year for bivoltine, etc.) that it can be neglected — probably a rare circumstance — failure to take it accurately into account will certainly cause systematic error.

Habitat, Distribution, and Behavior

The preferred habitat and spatial distribution of a species may have a profound effect upon estimation of secondary production. Many published production data were obtained from a given habitat, e.g. stream riffles, lake profundal — where obviously the data cannot apply to the entire water body; the value of such data is thus limited to certain ecological inferences or to methodological development (Waters and Crawford 1973). The influence of habitat preference is magnified and compounded when migratory or dispersal habits are such that a species population moves from one habitat to another, especially on a size-selective basis. Hall et al. (1980) studied a stream mayfly population (*Tricorythodes atratus*) in which the nymphs drifted on a regular basis from a riffle, on which they had hatched, downstream to a pool where they remained; the drifting nymphs were larger, on average, than the ones on the riffle, so that the pool population consisted of larger organisms. The error effect of calculating production from samples taken from only a riffle or a pool was substantial.

Molting and case-building habits also affect secondary production estimates, as exuviae and case materials are rarely accounted for (Castro 1975; Otto 1975), and serious underestimates may result.

Cannibalistic feeding behavior will result in an overestimate of production expressed as an energy flow rate, because part of the production estimated is the result of feeding on another part, i.e. a recycling of energy within the species. The error is probably small but depends upon the degree of cannibalism present in a species. It is an error similar to that in grouping two trophic levels in the Hynes method, but since, by definition, cannibalism occurs within one species, the error may occur in all methods.

Relative Quantification of Errors

All of the above potential for error would seem to leave a bewildering array of pitfalls into which the investigator in secondary production may fall. Obviously, some are quantitatively more important than others; some may be more commonly encountered than others. For the researcher viewing a particular scientific problem in the estimation of production, including the physical nature of the water body involved, the sampling equipment available, and the biology of the organisms for which production estimates are desired, it would be helpful to have a quantitative basis upon which to choose which errors need the greatest attention and, perhaps, which can be ignored as being relatively unimportant, all in relation to the precision and accuracy dictated by the objectives of the research. This section is intended to provide such a basis. As yet, data available are inadequate to provide a precise foundation for such quantification; consequently, the following attempt should be regarded as tentative and simply a working basis upon which I expect others to improve in the future. It is formulated, in large part subjectively, upon this writer's personal experience, the literature, and discussions/correspondence with many others.

Although not classified as life history features, or even always directly related thereto, sampling errors associated with taking benthic samples may be large, even overwhelmingly so. All benthic scientists are familiar with this fact and live with it constantly, at least with it threatening in the background, if not actively challenged by statistical tests and rigorous experiment. Included here is *sampling error*, in the statistical sense, which affects *precision*, and also *systematic errors* in sampling, such as failure to sample adequately all habitats or using a mesh size too large to capture small organisms, which affects *accuracy* usually in a known direction or sign. The *analytic errors* resulting from failure to account for the effect of life history features, discussed in this article, are also systematic errors which affect the estimate in a known direction. It should be further emphasized that some errors, particularly systematic errors of sampling and analytic errors related to life history, may be known and correctible; sampling error may be only measurable but not correctible (except by increasing the number of samples). It would seem prudent to make corrections for known errors of a given sign, although small, when sufficient life history information is available to do so.

First, combining two trophic levels — e.g. herbivore–detritivores and carnivores — essentially provides a meaningless datum. But if this is applied (in error) to the herbivore–detrivivore level, it would produce an overestimate of probably less than 10%.

Second, as indicated elsewhere above, voltinism appears to be the most important life history feature from the standpoint of making an over- or underestimate. For example, if an insect population were judged bivoltine when it was actually univoltine, the result by the Hynes method would be an overestimate of 100%; the converse (judging a bivoltine population as univoltine) would cause an underestimate of 50%.

Third, the grouping of species with different maximum–minimum sizes would result in a persistent though small error, an overestimate of about 10–20%. A similar error might result in using the Hynes method on a single species wherein the two sexes attain different maximum sizes.

Failure to take into account the CPI correction (Benke 1979) would cause an underestimate, I suggest on average, of approximately 20% (inferring an aver-

age of 20% of generation time in a nonproducing stage, a CPI of 0.8 × 365, or 292 d, for a univoltine species). This factor, however, has the potential of causing a much greater error in some species which have a much shorter CPI, perhaps an 80 or 90% underestimate for some mayflies, chironomids, and black flies.

Error due to the existence of cannibalism within a species would depend on the degree of cannibalistic behavior, but it probably would not exceed an overestimate of 10% (in terms of energy flow rates through a population).

Failure to estimate the losses of molting and silk making for an arthropod will produce an underestimate of energy flow rates. Castro (1975) and Otto (1975) indicate losses of about 25–30% for their caddisflies; however, this understimate may be much greater for other taxa that have more instars than the caddisflies, e.g. mayflies and crustaceans.

In general, use of the P/B ratio to make a crude (i.e. imprecise) estimate of production would be subject to about the same degree of error in the above cases. Selection of a cohort P/B of 5 would have the additional potential of about 15–25% error at most, since the P/B range appears to be about 4–6 for most benthic invertebrates.

Systematic errors related to distribution or behavior of the population are almost always underestimations and probably vary widely, but they have the potential of being very large. For example, Coleman and Hynes (1970) estimated that as much as 80% of benthic stream invertebrate populations may exist in the hyporheic zone of the stream bottom and is therefore not collected by traditional samplers, causing an 80% underestimate in standing stock and also probably production. Failure to collect smallest instars because of a large mesh size employed in a sampler also results in an underestimate, but not as great; with care, this error should probably not exceed 5 or 10%. Biasing sampling effort toward high or low population densities in different habitats obviously could result in high or low estimates; a thorough pre-sample knowledge of habitat preference and population distribution will help to avoid this kind of error, and sampling all habitats on a random or stratified-random basis (e.g. Resh 1977) will also reduce or eliminate this kind of systematic error.

Finally, sampling error (variance, standard error, confidence interval) represents perhaps the greatest problem, in part because in most cases nothing can be done to reduce it after the sampling operations are done with and the collected data tabulated and ready for analysis. Obviously, the best time to accommodate to this kind of error is prior to the initiation of the sampling schedule. Probably in the majority of cases in the past, sampling error simply has been ignored. Yet this may be so large that the 95% confidence limits far exceed the errors caused by most life history features and their associated systematic errors. Elliott (1977) has produced the definitive work on use of statistical analysis of macroinvertebrate data; more use of his analytical methods is hereby encouraged, in order to judge more properly the precision of benthic parameters, including production.

Future Needs

While published tables and summaries of voltinism for various taxa will continue to be extremely valuable for the secondary production investigator, of more direct need is the ability to determine, from field samples, the voltinism and length of CPI for the main species of concern. This will require an ability to sample the smallest specimens, to detect the existence of egg, pupal, or diapausing stages, and to distinguish and identify immatures. Certainly the ability to identify species from immature specimens will be a tremendous improvement. Development of culture facilities and procedures, both for identification of immatures and for determining various life history parameters, is a pressing and promising area of work.

The correctness of the Hynes method appears well established now, particularly since Benke's correction for CPI is made, but the usefulness of the method as a means of roughing out the production of an entire fauna appears diminished somewhat in view of the many groupings that must be made. It will continue to be extremely useful for many populations for which the earlier methods cannot apply but for which certain life history features still should be applied. However, if a researcher is willing to accept systematic errors in the range of up to about 25%, some of the life history features may be ignored, especially if sampling error is relatively high anyway.

Use of the P/B ratio would seem to have the broadest applicability, albeit with perhaps the least precision. Even so, trophic level, voltinism, and CPI still need to be known, at least approximately. A cohort P/B ratio of about 5 appears now to be the best figure to use for benthic invertebrates as one that is fairly constant; additional empirical data on P/B ratios for various taxa should be accumulated, especially for noninsect groups.

Acknowledgments

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Zooplankton Population Dynamics and *Diaptomus* Production in Waldsea Lake, a Saline Meromictic Lake in Saskatchewan

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SWIFT, M. C., AND U. T. HAMMER. 1979. Zooplankton population dynamics and *Diaptomus* production in Waldsea Lake, a saline, meromictic lake in Saskatchewan. J. Fish. Res. Board Can. 36: 1430–1438.

Zooplankton population dynamics were monitored in meromictic saline Waldsea Lake, Saskatchewan, during 1974–75. The dominant zooplankton species were *Diaptomus connexus*, *Brachionus plicatilis*, *Hexarthra fennica*, and *Daphnia similis*. *Diaptomus* had a 1-yr life cycle. Overwintered late-stage copepodites molted into adults in May and June and were followed by sequential peaks in numbers of eggs, nauplii, and copepodites. The estimated annual production of this species was 0.6 g dry weight·m^{-2} or 0.3 g C·m^{-2}. About 4% of the annual planktonic primary production would be required to support *Diaptomus* if it is 10% efficient. The standing crop of *Brachionus* and *Hexarthra* was highest in the spring and declined thereafter; *Hexarthra* was more abundant than *Brachionus*. The standing crop of *Daphnia* was much lower than that of either rotifer and showed a spring and fall peak in abundance. Differences in vertical distribution were present among the zooplankton species but no real vertical migrations were observed.

Key words: Diaptomus connexus, zooplankton, population dynamics, production, saline meromictic lake

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La dynamique des populations zooplanctoniques a été suivie dans le lac Waldsea, un lac salé méromictique de la Saskatchewan, en 1974–75. Les zooplanctontes dominants sont : *Diaptomus connexus*, *Brachionus plicatilis*, *Hexarthra fennica* et *Daphnia similis*. Le cycle biologique de *Diaptomus* est d'un an. Les stades copépodites tardifs qui ont passé l'hiver se transforment en adultes en mai et juin, et sont suivis de pics successifs du nombre d'oeufs, de nauplii et de copépodites. La production annuelle estimée de cette espèce est de 0,6 g de poids sec·m^{-2} ou 0,3 g C·m^{-2}. Avec une efficacité de 10%, il faudrait environ 4% de la production primaire planctonique annuelle pour maintenir la population de *Diaptomus*. La biomasse de *Brachionus* et *Hexarthra* est maximale au printemps et décline par la suite; *Hexarthra* est plus abondant que *Brachionus*. La biomasse de *Daphnia* est beaucoup moindre que celle de l'un ou l'autre rotifère et exhibe un pic d'abondance au printemps et en automne. Il existe, parmi les espèces zooplanctoniques, des différences de distribution verticale mais nous n'avons pas observé de migrations verticales réelles.

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PRODUCTION processes in saline lakes have not been extensively studied. Early studies of saline lakes emphasized physical–chemical characteristics and related them to the flora and fauna present. Recent studies have measured primary production in saline lakes in Africa, Australia, and North America (for example: Hamilton 1963; Wetzel 1964; Aleem and Samaan 1969; Culver and Brunskill 1969; Talling et al. 1973; Walker 1973, 1975; Haynes and Hammer 1978). Most of the lakes studied so far have had high rates of primary production. Except for the work of Walker (1973) and Paterson and Walker (1974) on Australian lakes and Swanson (1978) in a Canadian lake, there has been little research on secondary production in saline lakes. This is unfortunate because, as Williams (1972) has suggested, saline lake ecosystems are well-suited to trophic dynamic studies since they contain simple communities with few species and a simplified trophic structure.

Waldsea Lake is a saline, meromictic lake which meets Williams' suggested criteria for sites of trophic dynamic studies. Preliminary survey work (Hammer et al. 1975) suggested that Waldsea Lake would be suitable for studying the interaction of primary and secondary producers in a simple system. Of particular interest was the observation that despite a low phyto-

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plankton productivity Waldsea Lake appeared to support a relatively large standing crop of herbivorous zooplankton. To examine this relationship we monitored the population dynamics of herbivorous zooplankton in the lake and estimated the production of the most numerous species, *Diaptomus connexus*.

Description of Study Area

Waldsea Lake is a saline meromictic lake located near Humboldt, Saskatchewan, Canada (52° 17′ N, 105° 12′ W). The lake has an area of 464 ha, a maximum depth of 14.3 m, and a mean depth of 5.7 m. During 1974 surface conductivity ranged from 10 000 to 25 000 μmhos $\cdot$ cm^{-1} above the chemocline. A sharp chemocline at a depth of about 7–8 m separated the stable monimolimnion from the mixolimnion. Conductivity below 8 m varied between 40 000 and 50 000 μmhos $\cdot$ cm^{-1}. The water column was well oxygenated down to the chemocline. Below 8 m there was a high concentration of H_2S. A thermocline developed at about 4 m during the summer. Surface temperature reached 21°C but there was considerable wind-generated mixing; the top 4 m were often isothermal. The lake was frozen from mid-November to late April with up to 1.5 m of ice and snow cover.

At the time of this study the following zooplankton were present in the lake: a calanoid copepod, *Diaptomus connexus* Light; two rotifers, *Hexarthra fennica* (Levander) and *Brachionus plicatilis* (Müller); and a cladoceran, *Daphnia similis* Claus. Chironomid larvae (*Cricotopus ornatus Meigen*) and ostracods (*Cypriconcha ingens* Delorme) were abundant in the littoral zone. Two corixids (*Cenocorixa expleta* Uhler and *Trichocorixa verticalis interiores* Sailer) were also widely distributed in the lake. A harpacticoid copepod, *Onychocamptus mohammed* Blanchard and Richard, and an unidentified cyclopoid copepod were occasionally found in the plankton. The corixids, chironomids, ostracods, harpacticoid and cyclopoid copepods were not studied.

Methods

Zooplankton population dynamics were monitored weekly in 1974 from the time the lake thawed until it froze, a few times during the winter, and after the lake thawed in April 1975. Ten permanent sampling stations were placed randomly in the lake where the depth was greater than 9 m. Samples were collected using vertical hauls taken from below the chemocline (9 m) to the surface. One vertical haul was taken per station using a plankton net with a 25 cm mouth and a No. 20 (0.08 mm) nylon net. Absolute net efficiency was not known but was assumed to be constant between stations and dates. Samples were preserved immediately in a formalin–acetic acid–alcohol solution (FAA). Bulk plankton for dry weight and length measurements was collected using horizontal hauls on the same day as the vertical hauls. These samples were returned to the laboratory and stored at 4°C until used.

Weekly plankton samples were counted for all zooplankton species except for *Diaptomus* which was separated by developmental stage. The number of eggs per female was counted for every female carrying eggs in a sample; there were few loose egg clusters. When standing crops were high all counts except the number of eggs per female were done on subsamples.

Dry weights of the copepod developmental stages were measured on a Cahn Gram Electrobalance. Animals used for dry weights were killed in FAA and rinsed with freshwater before sorting. Males, females (without eggs), copepodites, nauplii, and eggs were weighed separately on each sampling date when they were abundant. Five samples of 10–150 individuals of each developmental stage were weighed on each sampling date. The number of individuals weighed in each of the five samples depended on the size of the individuals being weighed and was adjusted so that sample weight was large relative to the tare weight; i.e., eggs, nauplii, and small copepodites had many individuals per sample, and males, females, and large copepodites had fewer individuals per sample. Individual dry weight was calculated from the sample dry weights and number of individuals per sample and a mean individual dry weight for each developmental stage on each date was calculated from the individual dry weights of the five samples.

The diel vertical distribution of all the zooplankton species was examined on July 29–30. Samples were taken at station 2 every 3 h for 24 h. Sampling was done at 1-m intervals from 0 to 9 m inclusive using a 3-L Van Dorn bottle. These samples were preserved and counted in the same way as the weekly samples.

Diaptomus egg development time was determined at several temperatures following the method used by Burgis (1970). Females carrying egg clusters were collected and incubated at 6, 10, 15, and 20°C. The mean development time from laying to hatching at each temperature was determined by plotting the number of unhatched egg clusters against time from the beginning of the experiment and extrapolating this line to the time axis. These values were used in the production calculations to adjust egg development time (t_e) for ambient temperature.

Diaptomus production was estimated following the methods outlined in Winberg et al. (1971). Their formula (21) for the estimation of daily population production was modified by combining the terms for the production of nauplii and copepodites as follows:

$$P = \frac{(N_e)(W_e)}{t_e} + \frac{(N_j)(\Delta W_j)}{t_j}$$

where P is production in units of weight per square metre on a sampling date; N_e and N_j are the numbers of eggs and juvenile copepods (nauplii and copepodites) present on the sampling date expressed as numbers per square metre; W_e is the average egg weight and ΔW_j is the weight increment of juveniles expressed in weight units; t_e and t_j are the development times of eggs and juveniles in days. Nauplii and copepodites were combined as juveniles because the development time of nauplii was unknown. Juvenile development time (t_j) was approximated as the time from egg to adult and was set at 350 d. Juvenile weight increment was assumed to be the difference between average egg weight and average adult weight. Following Winberg et al. (1971) the P values for two successive sampling dates were averaged before multiplying by T to calculate the total production in that time interval. Production during the whole study period was taken as the sum of the production values estimated for successive sampling intervals.

Species determinations followed Edmondson (1959) and Ruttner-Kolisko (1972). Dr R. S. Anderson verified the *Diaptomus* identification.

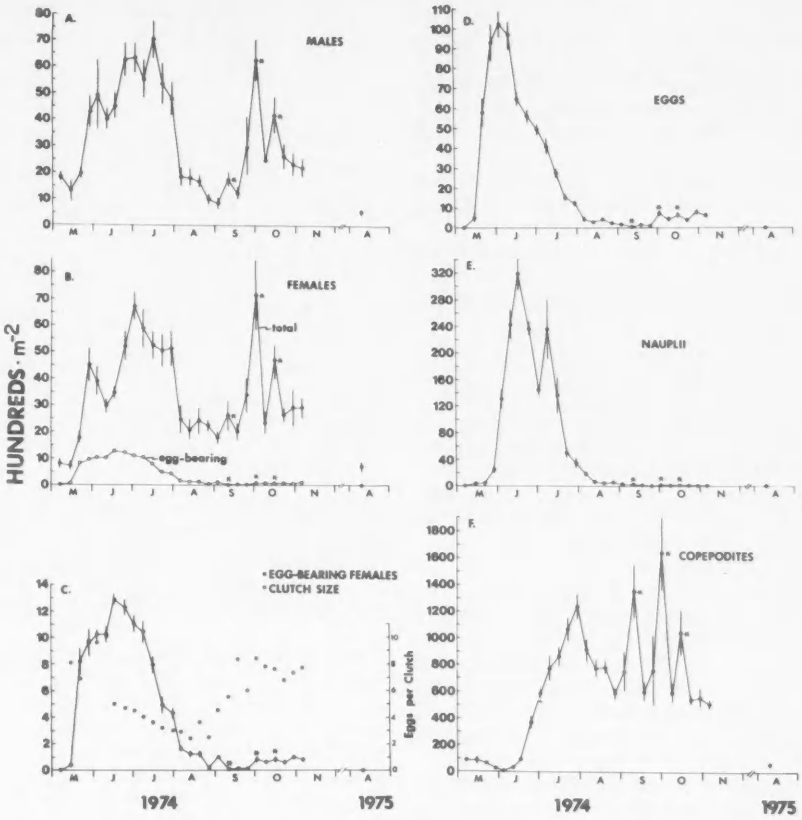

FIG. 1. Standing crops of *Diaptomus* developmental stages in 1974. A) males, B) total females and egg-bearing females, C) egg-bearing females and clutch size (numbers of eggs per clutch), D) egg, E), nauplii, F) copepodites. The data points are mean numbers per square metre above the monimolimnion. The vertical lines are ± SE. If no vertcial lines are shown, ± SE is within the data point. The asterisks mark dates on which sampling problems caused overestimates of population size.

Results

ZOOPLANKTON POPULATION DYNAMICS

Diaptomus has a 1-yr life cycle in Waldsea Lake. The overwintering copepodites molt into adults in May and June and are followed by sequential peaks in numbers of eggs, nauplii, and copepodites. The number of males and females increased to a peak in late spring–early summer, declined during August and early September, then increased somewhat in late September–October (Fig. 1A, B). Extremely windy conditions on September 11 and October 2 and 16 caused the vertical hauls to be somewhat diagonal. Population estimates based on these samples were therefore overestimated (asterisks in Fig. 1, 2, and 5). Overestimates of the population size on these dates is responsible for the wide fluctuations in numbers of adults and copepodites (Fig. 1A, B, F). The spring peak was the result of recruitment of adults from copepodites. The increase in number of adults (about 4000 males and 4000 females · m^{-2}) was approximately equal to the decrease in number of copepodites during May and early June. The cause of the fall increase in adults is not clear.

Most egg production occurred during May, June, and July (Fig. 1C, D). During this period the clutch size decreased from about 8 to 10 eggs in May and early June to about three by the end of July (Fig. 1C). This decline appeared to be correlated with a concomitant decrease in female weight (Fig. 4) and length. The percentage of females carrying eggs was highest in late May and early June (Fig. 1B). Even during the period of maximum egg production in May, June, and July egg-bearing females were less than 50% of the females present. The number of egg-bearing females decreased

drastically after July (Fig. 1B, C), but they were present throughout the summer. Many of the eggs in these clutches appeared abnormal in size, shape, or coloration. During September and October the number of egg-bearing females increased slightly and the clutch size increased also. These clutches were normal in appearance.

Shortly after the appearance of egg-bearing females in the population nauplii appeared and increased rapidly. Highest numbers of nauplii were found in June (Fig. 1E). By late July the sharp decrease in numbers of nauplii marked the decrease in egg production and recruitment into copepodites which occurred at this time. Copepodites decreased from overwintering levels to near zero in early June then increased to a peak in July (Fig. 1F). There was a gradual decrease in the number of copepodites after July. The three peaks in late September–October are the result of the sampling difficulties mentioned above. The decrease in numbers of copepodites between November and April suggests a considerable winter mortality. The number of overwintering copepodites was about the same in 1974 and 1975.

The number of *Hexarthra* increased rapidly in late May and reached a maximum of about $110\,000 \cdot m^{-2}$ by mid-June (Fig. 2A). The population size decreased rapidly in July and then gradually declined throughout the rest of the year. The *Brachionus* population followed a similar pattern (Fig. 2B). *Brachionus* was less abundant than *Hexarthra* and reached its peak density later in the summer. The decline in the *Brachionus* population was less precipitous than that in *Hexarthra* and the densities of the two rotifers were similar during late summer and fall. Late fall fluctuations in rotifer standing crop due to sampling problems were less noticeable than in *Diaptomus* but can be seen in *Hexarthra*.

Daphnia population size peaked in June, declined in mid-August, and stayed relatively low the rest of the fall except for fluctuations due to sampling problems. The maximum density of *Daphnia* was much lower than that of either rotifer or *Diaptomus*.

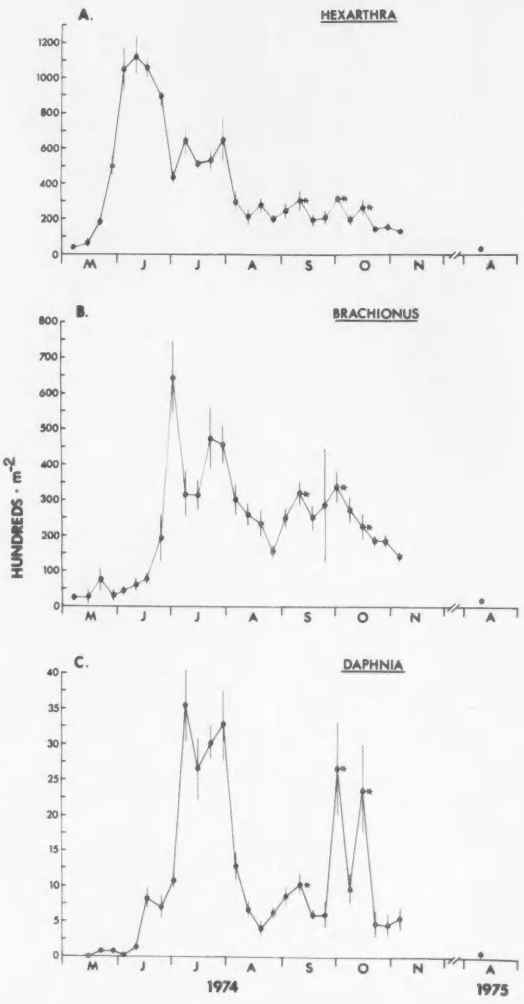

FIG. 2. Standing crops of *Hexarthra*, *Brachionus*, and *Daphnia* in 1974. The data points are mean numbers per square metre above the monimolimnion. The vertical lines are ± SE. Asterisks as in Fig. 1.

VERTICAL DISTRIBUTION

Vertical distribution was examined when all the *Diaptomus* developmental stages were present. Although there were differences in vertical distribution among the zooplankton species and copepod developmental stages there was little evidence of diel vertical migrations (Fig. 3). For all practical purposes there were no zooplankton below the chemocline, i.e. 7–8 m. Those few animals collected at 9 m were dead or moribund. *Diaptomus* males, females, and copepodites were distributed throughout the water column above 9 m at all times. Most nauplii were found in the top 4 m. Females carrying eggs had a variable distribution; they appeared to be nearer the surface from 18:00 to 03:00 and nearer the chemocline from 06:00 to 15:00.

Most *Daphnia* were found above 5 m and did not make any appreciable diel change in position. *Brachionus* was only found below 4 m; *Hexarthra* was found throughout the water column to a depth of 8 m but the bulk of the population was below 4 m. Neither rotifer made extensive diel vertical movements.

DIAPTOMUS WEIGHT AND PRODUCTION

Adult dry weight varied seasonally (Fig. 4). Adult dry weight was highest in June. In May adult males and females weighed the same; in June and July females were larger than males. Adults were not weighed directly

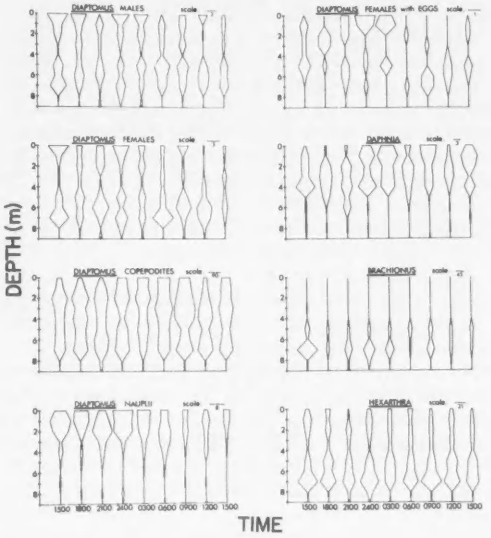

FIG. 3. Diel vertical distribution of zooplankton in Waldsea Lake on July 29–30, 1974. The scale bars represent the number of individuals per litre.

during September, October, and November when they were rare in the plankton. Calculations from length–weight curves for adults suggest an adult dry weight of about 5 μg/individual for those adults present during this period. The overall average adult weight was taken as 9.2 μg ($n = 28$; values for males and females on 14 dates). Egg weight was relatively constant during the spring egg production period (Fig. 4). Average egg weight was 0.8 μg ($n = 5$ dates); this value was used as W_e in the production calculations. Average nauplius weight was relatively constant also (Fig. 4). Average copepodite weight was high in May when late stage copepodites were present before becoming adults. From June on there was a gradual increase in the average copepodite weight (Fig. 4). The weight increment of juvenile copepods ($\Delta W_j = 8.4$ μg) used in the production calculations is the difference in weight between the final egg weight (0.8 μg) and average adult weight (9.2 μg).

Daily production estimates were highest in July (Fig. 5). Egg production was a large part of total production only during late May and June. By mid-July egg production was declining and copepod production was primarily growth of nauplii and copepodites. By August egg production made a negligible contribution to total production. Daily production estimates varied around 1.5 mg·m^{-2}·d^{-1} from August to November and may have decreased slightly over this period. The three peaks in September and October are due to overestimates of population size on September 11 and October 2 and 16. The estimated annual production was 0.6 g dry weight·m^{-2}.

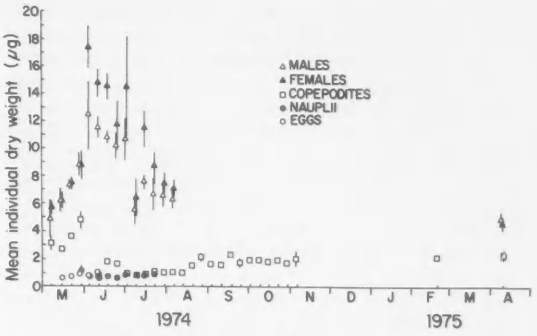

FIG. 4. Dry weights of *Diaptomus* developmental stages in 1974–75. The data points are mean individual dry weights from five samples on each date. The vertical lines are 95% confidence limits. If no vertical lines are shown the 95% confidence limits are within the data point.

Discussion

In Waldsea Lake the bulk of the *Diaptomus* population has a 1-yr life cycle. Eggs are produced primarily in spring, the naupliar and early copepodite stages are completed in summer, and the population overwinters as late stage copepodites. The source of the small increase in adults during late fall is not clear. Late-stage copepodites which are small in size are known to molt into adults and reproduce instead of overwintering (I. A. McLaren, Dalhousie Univ., personal communication). Such individuals would be producing a second generation which would overwinter as nauplii or early-stage copepodites. The fall increase in adults could also be derived from a subpopulation of *Diaptomus* which hatches in the fall, overwinters as nauplii or early-stage copepodites and stays out of phase with the bulk of the population until they reproduce the following fall. Whatever the source, there is some evidence from dry weight data of a small cohort of copepodites out of phase with

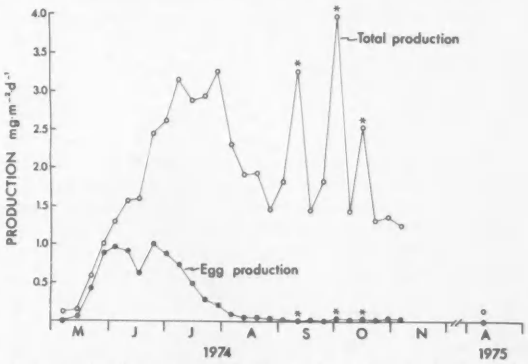

FIG. 5. Daily egg production and total production estimates for *Diaptomus* on sampling dates in 1974–75. Asterisks as in Fig. 1.

the rest of the population. Copepodite dry weights were high in May because of a preponderance of large late stage copepodites. The presence of low numbers of small copepodites at this time would not have been evident from the dry weight data because all copepodite stages were pooled. Similarly, detection of a small cohort of relatively larger copeodites present in the summer would not have been possible against the overwhelming number of very small early-stage copepodites. The presence of copepodites with dry weights of about 1.5 μg in late June when very few copepodites were present in the lake and the correspondence between coppodite weight and nauplius weight in July suggests that these copepodites are a cohort which hatched in late fall. They were apparently too small to become adults in May, yet were too big to be individuals recently recruited from nauplii in June. If this is the case, they could be the source of the approximately 5 μg adults found in September and October.

The increase in adult weight throughout May and June was due to recruitment of copepodites which were growing over this period and to the accumulation of reproductive products by adults. In June and July females were longer and heavier than males, and the weight differential between them was about equal to the weight of an egg clutch. The decrease in weight of both males and females in mid-June coincided with an increase in water temperature to above 16°C. The decrease in adult weight was associated with a sharp drop in clutch size and a decrease in adult length which occurred at the same time. The sharp decrease in clutch size in Waldsea Lake occurred when the surface temperature was 16–20°C. A sharp decline in clutch size when water temperature was 15°C or greater was found in several *Diaptomus* species in Saskatchewan by Sawchyn and Hammer (1968). Water temperature in the top few metres had decreased to about 15°C in September when the clutch size increased again. The fall increase in clutch size in *D. connexus* in Waldsea Lake was greater than that found by Sawchyn and Hammer (1968) for other *Diaptomus* species.

Estimates of *Diaptomus* daily production on each sampling date are based on formulae for estimating production of populations with continuous reproduction (Winberg et al. 1971). These formulae were chosen at the beginning of the study because the reproductive periodicity of *Diaptomus* was unknown and the extended breeding season made it difficult to follow a cohort. By combining nauplii and copepodites as juveniles we have assumed their growth rate is the same. It is not clear how this assumption biased the production estimates. By assigning a duration time of 350 d for juveniles we have assumed a linear growth rate for that period. Weight gain by nauplii and copepodites appeared to be more or less linear during the summer and fall of 1974. When the lake is ice covered this assumption is not valid and our daily production estimates are underestimated because the constant $\Delta W_j/t_j$ is a smaller value than it would be if a shorter development time were used. However, the assumption of linear growth has little effect on the estimate of total production for the year.

Despite these problems the daily production estimates on each sampling date illustrate the seasonal pattern of *Diaptomus* production. Egg production is only an appreciable fraction of total production during May and June even though clutch size increased fourfold from August to September and some egg-bearing females were present. The sharp decline in total production in August is due principally to a decrease in the number of copepodites. This decrease is not accounted for by recruitment into adults. The source of this mortality is not known. The three peaks in September and October are artifacts caused by sampling problems.

The zooplankton standing crop in Waldsea Lake was not high. The standing crop of *Diaptomus* developmental stages was about the same as that of *Diaptomus sicilis* in Fayetteville Green Lake, a temperate meromictic lake with a comparable annual phytoplankton primary production rate (Culver and Brunskill 1969). Despite the similarities in *Diaptomus* standing crop between the two lakes, Fayetteville Green Lake supported more zooplankton species with a greater overall standing crop.

Direct comparisons of rotifer standing crops are possible with Lake Werowrap, a shallow saline lake in Australia. Maximum concentrations in Lake Werowrap (Walker 1973) were about three times as great for *Hexarthra jenkinae* compared to *Hexarthra fennica* and about 200 times as great for *B. plicatilis* on an areal basis as in Waldsea Lake. However, Werowrap had a maximum depth of only 1.14 m at the time of peak populations of rotifers. These large differences were maintained even though phytoplankton production in Lake Werowrap was only about 11 times that of Waldsea Lake.

Comparable secondary production data for zooplankton is not available for other saline lakes. The annual production of *Diaptomus* was twice the annual production of the chironomid *Cricotopus ornatus* (Swanson 1978), the most abundant benthic animal in Waldsea Lake. In Lake Werowrap chironomid production was more than two orders of magnitude higher (Paterson and Walker 1974).

Primary production in Waldsea Lake is low. Phytoplankton production was 38 g $C \cdot m^{-2} \cdot yr^{-1}$, the lowest of seven saline lakes examined by Haynes and Hammer (1978). This is an average production of about 200 mg $C \cdot m^{-2} \cdot d^{-1}$ ($n = 7$, range = 53–345) for the open water period. This production rate was roughly half that of neighbouring meromictic Deadmoose Lake studied at the same time. Bacterial primary production in Waldsea Lake was estimated to be about 32 g $C \cdot m^{-2} \cdot yr^{-1}$ (Lawrence et al. 1978). Thus Waldsea Lake has only one-fourth of the total planktonic primary production reported for Fayetteville Green Lake (51 g $C \cdot m^{-2} \cdot yr^{-1}$ algal, 239 g $C \cdot m^{-2} \cdot yr^{-1}$ bacterial) by Culver and Brunskill (1969) and about one-sixth

that reported for Lake Werowrap by Walker (1973).

Using the production estimates for *Diaptomus*, it is possible to make a preliminary examination of the relationship between secondary production and phytoplankton production in Waldsea Lake. Annual production was estimated to be 0.6 g dry weight for *Diaptomus*. Assuming the carbon content of zooplankton to be 44% of dry weight (Wright 1965), *Diaptomus* production was 0.26 g $C \cdot m^{-2} \cdot yr^{-1}$. If one assumes an ecological efficiency of 10% (Mann 1969), consumption of 2.6 g $C \cdot m^{-2} \cdot yr^{-1}$ was required. This is about 7% of the estimated annual phytoplankton production in this lake.

This estimate of the proportion of annual phytoplankton production required for secondary production is a minimum estimate for two reasons. Not all phytoplankton production is directly available to herbivorous zooplankton (Porter 1972, 1973). Secondly, other herbivorous zooplankton and possibly some benthic fauna also have direct or indirect access to planktonic primary production.

The extent to which bacterial primary production in Waldsea Lake is utilized by zooplankton is unknown. The photosynthetic, green sulfur bacteria which form the bacterial "plate" at the chemocline in Waldsea Lake are extremely numerous. Analysis of water from the "plate" showed an ATP concentration of 0.1 $\mu g \cdot 50$ mL^{-1}; this equals 1.03 $\mu g\ C \cdot L^{-1}$ as cellular carbon and is five times higher than the highest value previously measured (H. Paerl, University of California, Davis, CA, personal communication). Bacterial production in Waldsea Lake was estimated to be 46% of total planktonic primary production. Previous studies have shown that zooplankton are often found in close proximity to the bacterial "plate" (Sorokin 1965; Culver and Brunskill 1969) and that zooplankton feed on these bacteria (Sorokin 1966; Takahashi and Ichimura 1968). It is suggestive that in Waldsea Lake *Diaptomus* and both species of rotifers are found in the bacterial plate although numbers there are small. While no diel vertical migrations were found, all *Diaptomus* developmental stages were found down to the depth of the bacterial plate.

There are several other sources of organic carbon which could be utilized by herbivores in Waldsea Lake. Two vascular hydrophytes (*Ruppia occidentalis* and *Potamogeton pectinatus*) and the attached algae (*Chara* spp. and *Rhizoclonium hieroglyphicum*) are present in the littoral zone (Hammer et al. 1975). No measurements of primary production of these plants are available. *Rhizoclonium*, at least, is an important food of chironomids (Swanson 1978). The input of allochthonous organic material into Waldsea Lake is potentially large. The lake is surrounded by farmland under intensive cultivation. Pollen deposition on the lake during the summer and organic material left after harvesting and carried into the lake by runoff are the major sources of allochthonous organic carbon. No estimates of the magnitude of this carbon input are available. The degree to which the various sources of organic material are utilized and the routes by which they are made available to herbivores need to be studied further. The simplified trophic structure of Waldsea Lake makes it particularly suitable for such studies.

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Différenciation de populations anadromes et dulcicoles de Grands Corégones (*Coregonus clupeaformis*) par la composition minérale de leurs écailles

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MOREAU, G. ET C. BARBEAU. 1979. Différenciation de populations anadromes et dulcicoles de Grands Corégones (*Coregonus clupeaformis*) par la composition minérale de leurs écailles. J. Fish. Res. Board Can. 36: 1439–1444.

On a étudié la composition minérale en éléments alcalino-terreux d'écailles de Grands Corégones d'eaux douces et d'eaux salées dans la région de la rivière La Grande. Alors que les teneurs en calcium et en magnésium demeurent inchangées, quelque soit le site ou l'âge, les teneurs en strontium changent appréciablement selon le bassin et la salinité de l'eau. Les variations en strontium sont utilisées pour différencier les populations anadromes et dulcicoles et pour caractériser certains secteurs de la rivière La Grande.

Mots clés: Grands Corégones, strontium, calcium, magnésium, écailles, populations anadromes et dulcicoles

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The mineral composition in alkaline earth elements of whitefish scales from fresh- and saltwater of the La Grande River area were studied. While calcium and magnesium concentrations remained unchanged, regardless of site or age, the strontium concentrations changed markedly according to basin and water salinity. The variations in strontium are used to differentiate anadromous and freshwater populations, and to caracterize certain portions of La Grande River.

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LE Grand Corégone (*Coregonus clupeaformis*) est surtout connu par ses populations de lacs et de rivières mais, dans les régions nordiques, il n'est pas rare de le rencontrer en eau saumâtre dans les estuaires et dans les baies. Il peut être important, notamment par rapport aux travaux d'aménagement, de connaître si les individus d'une rivière appartiennent tous à une population migratrice ou se répartissent en deux populations: l'une sédentaire dulcicole, l'autre migratrice amphibiotique.

Une telle question se pose à propos de la rivière La Grande, Québec, Canada, où le Grand Corégone est présent à tous les niveaux, y compris dans son estuaire, ainsi que dans la zone côtière de la Baie de James. Dans ce cas, la limite d'une population strictement dulcicole pourrait être établie par un rapide, situé à 37 km de l'embouchure (site B, fig. 1), dont les caractéristiques physiques correspondent aux limites des possibilités de nage des Grands Corégones telles qu'établies par Jones *et al.* (1974).

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Pour répondre à cette question, la technique décrite par Bagenal *et al.* (1973) est employée et complétée par une étude plus poussée de la minéralisation des écailles.

Matériel et méthodes

Les spécimens utilisés ont été prélevés dans différents sites du territoire de la Baie de James (fig. 1): région de Black Island (A) de salinité d'environ 20‰, immédiatement en aval (B′) et en amont (B″) des premiers rapides, en amont d'une série de rapides (C, D″) dont certains incontestablement infranchissables et enfin, à titre comparatif, dans 2 lacs (D′, E) de la même région et dans un lac (F) sans communication avec le réseau hydrographique de la rivière La Grande.

Les écailles prélevées lors de la capture ont été conservées à sec jusqu'au moment de l'analyse de la composition minérale.

L'analyse de la teneur en strontium s'inspire de la méthode de Bagenal *et al.* (1973). On pèse une ou plusieurs écailles pour obtenir un poids voisin de 5 mg. Bien que la reproductibilité des résultats en strontium demeure bonne avec des échantillons de moins de 2 mg et d'aussi peu que 0,5 mg, on observe des écarts d'analyse prononcés sur le

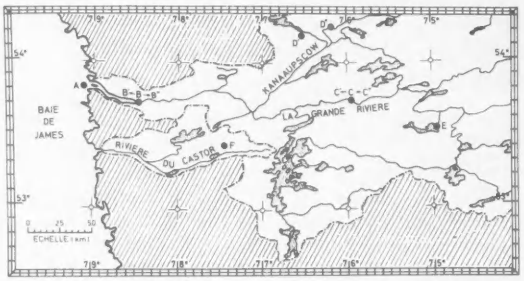

FIG. 1. Localisation des sites de prélèvement des Grands Corégones.

dosage en calcium et en magnésium lorsque le poids d'échantillon est inférieur à 2 mg. La matière organique est décomposée par oxydation avec 0,5 cm^3 de $HClO_4$ à 60°C pendant 1 h. La solution est ensuite évaporée par ébullition et le résidu repris par 5 cm^3 de HNO_3 0,1 mol/L pendant environ 1 h à 60°C; le volume de la solution est ensuite complété à 10 cm^3.

Le dosage du strontium s'effectue par absorption atomique en utilisant un volume variant entre 10 et 25 μL. En raison des interactions résultant de la présence de fortes concentrations de calcium et de magnésium dans la solution acide, le caractère de la flamme et les paramètres instrumentaux en absorption atomique sont très difficiles à choisir. Pour contourner ces difficultés, la fournaise au graphite Perkin Elmer HGA, montée sur le spectrophotomètre Perkin Elmer 305, est utilisée avec une température de calcination de 800°C (28 s) et une température d'atomisation de 2500°C (12 s). La courbe d'absorption est linéaire pour les concentrations analysées (0–0,2 mg/L de strontium) et la présence des ions calcium (0–100 mg/L), magnésium (0–20 mg/L), phosphate (0–100 mg/L) ou potassium (0–10 mg/L) n'affecte pas le signal du strontium. L'erreur sur la détermination du strontium est d'environ ± 10% pour les faibles concentrations et d'environ ± 5% pour les concentrations élevées. Cette erreur provient principalement de la lecture d'absorption dont la répétabilité se situe à ± 5%.

Pour le dosage du calcium et du magnésium, on prélève 1 cm^3 de la solution mère, on dilue à 10 cm^3 et on mesure l'absorption en flamme air-acétylène. Le calcium est mesuré à 422,7 nm en utilisant le brûleur dans une position tournée, correspondant à 100% d'absorption pour une concentration de 7 mg/L. La précision des résultats se situe alors à environ ± 10%. Le magnésium est dosé à 285,2 nm en utilisant des solutions étalons de 0 à 0,5 mg/L; la précision obtenue est de l'ordre de ± 5%.

En raison d'une certaine hétéroscédasticité, l'analyse de variance ne peut se faire sur les données brutes. L'écart-type des moyennes de groupes tendant à être proportionnel à la moyenne, la transformation logarithmique paraissait la plus indiquée dans les circonstances. Le tableau des données brutes et transformées peut être obtenu, pour un coût minime, en s'adressant au Dépôt des données non-publiées, CISTI, Conseil national de recherches du Canada, Ottawa, Ont. K1A 0S2.

Résultats et discussion

Le diagramme de distribution (fig. 2) montre une dispersion des concentrations en strontium plus importante chez les individus prélevés dans la baie que dans tous les autres sites de prélèvement. De plus, la teneur moyenne en strontium chez les poissons prélevés en eau salée (A) est supérieure (au moins 1,5 fois) à celle observée chez les spécimens d'eau douce (tableau 1). Cette

TABLEAU 1. Valeurs moyennes et étendues des concentrations et des rapports massiques, suite à la transformation logarithmique des données.

		Valeurs moyennes et étendues					
Groupe	n	Sr $\mu g/g$	Mg $\mu g/g \times 10^{-1}$	Ca $\mu g/g \times 10^{-3}$	Ca/Mg	Ca/Sr	Mg/Sr
A	31	605 470–779	252 202–314	108 95–123	42 34–53	175 132–233	4,1 2,9–5,9
	68[a]	626 486–807					
B	34	443 367–534	245 213–281	111 96–129	46 40–53	251 128–319	5,5 4,3–7,2
	58[a]	455 372–556					
C	22	340 252–457	203 170–242	91 68–121	43 36–51	266 206–344	6,3 4,6–8,6
D	17	428 376–487	217 185–234	105 97–114	49 45–53	244 209–284	5,0 4,3–5,8
E	20[a]	377 318–446					
F	12	212 178–254	219 205–233	108 101–115	49 45–54	508 413–625	10,3 8,6–12,2

[a]Ensemble des spécimens pour lesquels la concentration en strontium est connue.

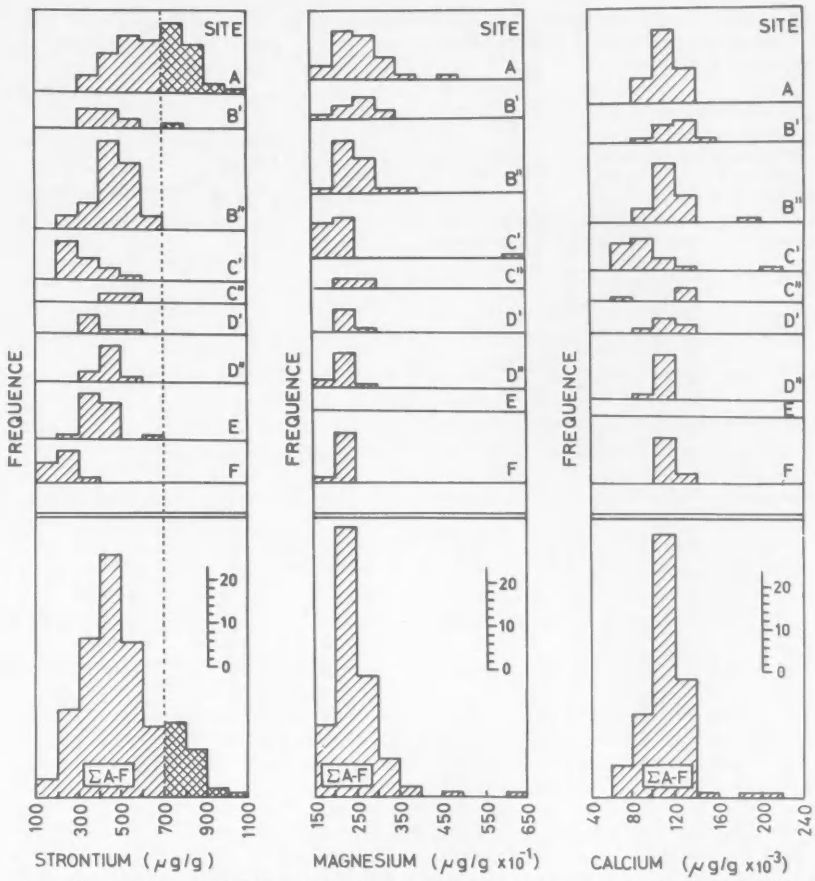

FIG. 2. Distribution des Grands Corégones selon les concentrations et les sites de prélèvement. Les hachures croisées indiquent les spécimens considérés d'eau salée.

différence entre Grands Corégones d'eau douce et d'eau salée est du même ordre que celle observée par Bagenal *et al.* (1973) chez les Truites.

Puisque le site B se situe en eau douce, qu'il est voisin du site A en eau salée et qu'il est associé à un nombre élevé de spécimens, l'analyse de variance en fonction de ce site pourrait répondre à la question de la variabilité des concentrations minérales des écailles en fonction de la région. Le tableau 2 montre que les populations des sites A, C et E, du bassin de la rivière La Grande, se distinguent de celles du site B par leur teneur en strontium. La comparaison impliquant les rapports massiques Ca/Mg, Ca/Sr et Mg/Sr indique, cependant, que seulement la population du site A peut être considérée distincte de celle de B, si on limite l'étude au bassin hydrographique de la rivière La Grande.

La distinction entre les spécimens d'eau salée (A) et ceux d'eau douce apparaît également lorsque la comparaison se fait par groupes d'âge. L'analyse de variance (tableau 3) fait ressortir: (1) l'homogénéité des teneurs moyennes en strontium chez les spécimens d'eau douce âgés de 2 à 8 ans; (2) la diminution continue en stron-

TABLEAU 2. Analyse de variance des données transformées. Comparaison entre le groupe B et les autres groupes.

	Paramètre[b]					
Groupe	Sr	Mg	Ca	Ca/Mg	Ca/Sr	Mg/Sr
A	**	n.s.	n.s.	n.s.	**	**
C	**	**	—	n.s.	n.s.	n.s.
D	n.s.	—	n.s.	n.s.	n.s.	n.s.
F	**	—	—	n.s.	**	**
E[a]	**					

[a]Les valeurs de Mg et Ca correspondantes ne sont pas disponibles.

[b]**: différence hautement significative ($P < 0{,}01$); n.s.: difference non significative; —: variances ne permettant pas une analyse comparative.

TABLEAU 3. Analyse comparative selon l'âge et les concentrations en strontium des specimens des groupes A et B, C, E, suite à la transformation des données.

Age	Concentrations moyennes et étendues en Sr(μg/g) Groupe A $\bar{x}(n)$ étendue	Groupe B, C, E[a] $\bar{x}(n)$ étendue	Analyse de F[b]
2	645 (3) 602–692	433 (13) 372–488	**
3	679 (15) 534–863	473 (11) 395–567	**
4	652 (14) 513–830	450 (14) 358–561	**
5	508 (11) 404–638	473 (9) 412–545	n.s.
6	742 (12) 660–836	441 (10) 369–528	**
7	692 (6) 610–786	424 (4) 392–460	**
8	468 (7) 388–566	376 (3) 289–490	n.s.
2–8	626 (68) 486–807	446 (64) 372–535	**
9		399 (7) 337–473	
10–11		340 (10) 279–418	
12–13		293 (6) 235–330	
14–17		257 (6) 233–284	

[a]L'âge des spécimens du groupe D n'est pas connu.
[b]**: différence hautement significative ($P < 0,01$); n.s.: différence non significative.

tium, associée avec un vieillissement passé 8 ans; (3) une teneur moyenne semblable chez 5 des 7 groupes d'âge des spécimens d'eau salée; (4) une différence hautement significative entre les populations de même âge mais de milieux différents. La répartition des concentrations selon le milieu et l'âge, qui est présentée à la figure 3, montre que seules les populations de 5 et 8 ans dans la baie présentent des teneurs moyennes en strontium voisines de celles observées chez les spécimens de même âge dans la région d'eau douce. Les teneurs élevées en strontium chez les groupes d'âge de la baie doivent être associées au caractère d'eau salée de ce milieu (tableau 4), au même titre que les fortes concentrations en strontium des Truites d'eau de mer étudiées par Bagenal *et al.* (1973). Les spécimens prélevés dans le bassin hydrographique de la petite Rivière du Castor présentent par contre des teneurs en strontium nettement inférieures à celles observées dans tout le bassin hydrographique de la Grande Rivière. Avant d'établir des critères pour différencier des populations de Grands Corégones sur la base des concentrations en strontium de leurs écailles, il est apparu important de rechercher la composition en divers autres éléments

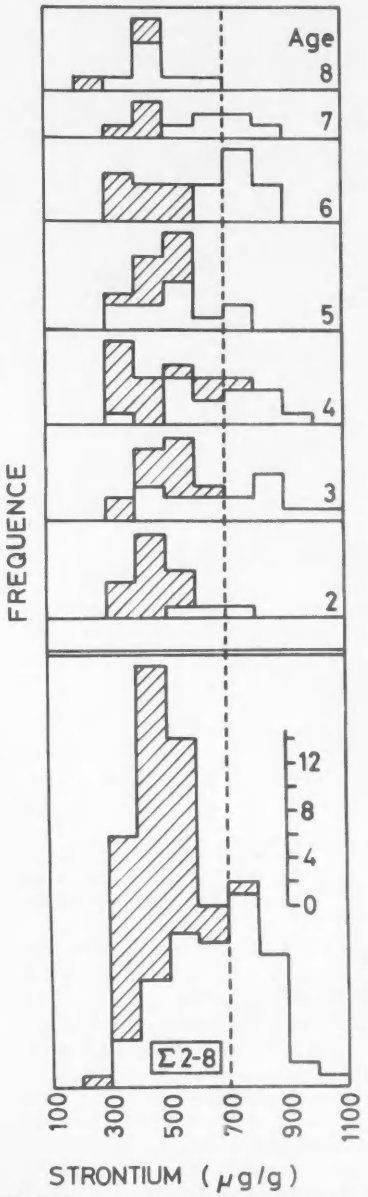

FIG. 3. Distribution des Grands Corégones selon la teneur en strontium et l'âge, dans la baie (partie non-hachurée) et la rivière (partie hachurée).

TABLEAU 4. Composition et rapports massiques d'éléments alcalino-terreux dans des eaux salées et douces.

Type	Strontium mg/L	Magnesium mg/L	Calcium mg/L	Mg/Sr	Ca/Sr	Ca/Mg
Eau de mer[a]	8	1350	400	170	50	0,3
Baie de James[b,e] (eaux salées)	3,6	880	240	250	70	0,3
Eau de rivière[c,e]	<0,05	2*–4**	10*–20**	>80	>400	5
La Grande[d,e] (eaux douces)	0,01	0,5	2	50	2000	4

[a]Ciaccio (1971).
[b]Environ 30 km au large de Fort George.
[c]*Rivière Chaudière, Québec; **Fleuve Saint-Laurent à Québec.
[d]Embouchure de la rivière Achazi 53°43′N–78°30′E.
[e]Gouvernement du Québec (1974).

minéraux et de comparer les concentrations moyennes selon les régions.

La distribution observée (fig. 2) dans les différents sites, tant du point de vue du calcium que du magnésium, ne présente pas les mêmes variations que celle du strontium. On obtient également des valeurs moyennes en calcium et en magnésium qui diffèrent peu (tableau 1) et qui, selon l'analyse de variance, peuvent être associées à des populations de même qualité (tableau 2). Bien que les rapports de variance, pour l'analyse, selon l'âge, des spécimens prélevés en B, C, E, permettent de conclure qu'il n'existe pas de variation significative dans les teneurs en calcium et en magnésium entre 2 et 9 ans, le rapport Ca/Mg s'avère préférable dans l'analyse comparative car les teneurs élevées ou faibles en calcium sont généralement reliées à des teneurs correspondantes en magnésium. Aussi bien les valeurs moyennes de Ca/Mg (tableau 1) que l'analyse de variance (tableau 2) soulignent la constante de ce rapport chez les différents groupes étudiés. L'analyse du rapport Ca/Mg chez les 46 spécimens prélevés en B, C, E, pour les 7 groupes d'âge compris entre 2 et 17 ans, montre que les Grands Corégones d'une même région assimilent les ions calcium et magnésium selon un rapport constant. Le calcul du rapport massique Ca/Mg permet donc de valider les résultats des analyses de calcium et de magnésium, tout en facilitant le rejet ou l'interprétation des données anormales.

Puisque le rapport Ca/Mg permet de ramener sur une base commune la comparaison entre plusieurs échantillons et plusieurs sites, les rapports massiques Ca/Sr et Mg/Sr pourraient aider à caractériser des spécimens selon leur site de prélèvement. Ainsi on constate (tableaux 1 et 2) que les populations de B, C et D sont semblables alors que celles de A et F sont différentes des trois précédentes et également différentes entre elles.

L'existence de deux populations distinctes de Grands Corégones dans la baie, à la sortie de la rivière La Grande, paraît évidente, si on compare les teneurs moyennes et la dispersion des concentrations en strontium dans le site A et dans les sites B, C, D et E. La présence de poissons venant de la rivière, parmi les spécimens pêchés dans la baie, affecte cependant la moyenne dans la baie et, en raison de l'étendue des concentrations chez les spécimens de la rivière, ne permet pas d'observer une distribution avec deux maxima. La sélection de critères de différenciation chez les spécimens de la baie devra donc se faire en utilisant des valeurs limites basées sur les concentrations observées en eau douce. Bien que Simmons (1971) et Fleming (1974) aient démontré expérimentalement l'existence d'un remaniement de strontium et de calcium dans les os et les écailles, Bagenal *et al.* (1973) ont prouvé que les fortes concentrations en strontium des Truites d'eau de mer ne changeaient pas après une exposition expérimentale de 60 j à l'eau douce. Il semble donc que les différences de concentrations résultant de l'exposition aux divers milieux soient suffisamment stables. Dans le cas des Grands Corégones de la baie qui viennent de la rivière, on devrait s'attendre à un acroissement graduel de la teneur en strontium de leurs écailles. De fait, seuls les spécimens qui ont séjourné longtemps dans l'eau salée peuvent contenir de fortes concentrations en strontium. La valeur limite en strontium sera donc maximale pour un spécimen d'eau douce mais éliminera de nombreux spécimens qui séjournent depuis un certain temps dans l'eau salée. En plus du critère de différenciation eau salée — eau douce basée sur la teneur en strontium (Sr $> 700\ \mu g/g$), on peut utiliser conjointement deux autres critères ($Ca/Sr < 200$ et $Mg/Sr < 4$) qui découlent du premier. Selon le critère de strontium, on constate (fig. 2) qu'un seul spécimen prélevé dans la rivière aurait séjourné dans l'eau salée. Ce spécimen ainsi que deux autres, qui présentent des rapports massiques inférieurs aux critères d'eau salée et dont les concentrations en strontium sont 550 et 580 $\mu g/g$, ont été pêchés dans le site B′ à la base du rapide, vers la fin de septembre. Les autres spécimens de B′ ont été pêchés au début du printemps et aucun d'eux n'obéit à un des trois critères d'eau salée. Ceci tendrait à démontrer, que les Grands Corégones remontent jusqu'à la base des rapides du kilomètre 37 pour hiberner, et que la dévalaison s'effectue au tout début de la fonte des glaces.

Des 31 spécimens de la baie dont l'analyse des trois paramètres minéraux a été faite sur un échantillon de plus de 2 mg, 10 suivent les trois critères d'eau salée. Parmi les 21 autres, 13 ont un rapport Ca/Sr inférieur

à 200 alors que 3 présentent des teneurs en strontium supérieures à 700 μg/g. Dans le cas des spécimens dont seulement le strontium a été dosé, 18 sur 37 sont conformes au critère d'eau salée.

L'influence de la composition chimique des eaux semble se manifester sur la distribution du strontium, en particulier, comme le laissent supposer, non seulement les données sur les Grands Corégones du bassin hydrographique de la rivière La Grande, mais aussi les travaux de Ophel et Judd (1967) et surtout les résultats du lac Nathalie (F) situé dans un bassin plus côtier et géologiquement différent de celui de la Grande (fig. 1). La connaissance de la composition minérale des écailles paraît un bon paramètre différenciateur des populations anadromes et dulcicoles de la même espèce. On peut conclure qu'il existe deux populations de Grands Corégones dans la rivière La Grande: l'une cantonnée dans la partie aval de la rivière, de l'embouchure aux premiers rapides et pouvant migrer dans l'estuaire et la baie, l'autre localisée au-dessus des premiers rapides et effectuant tout son cycle en eau douce, les seuls échanges entre ces deux populations se faisant par des mouvements de dévalaison. Bien que la teneur en strontium se révèle utile pour caractériser les Grands Corégones d'une région, il est cependant nécessaire de calibrer ce paramètre pour chaque système hydrographique sous étude.

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Intrusions and Vertical Mixing at the Shelf/Slope Water Front South of Nova Scotia

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HERMAN, A. W., AND K. L. DENMAN. 1979. Intrusions and vertical mixing at the shelf/slope water front south of Nova Scotia. J. Fish. Res. Board Can. 36: 1445–1453.

Intensive profiling of the shelf/slope water boundary south of Nova Scotia has been made with a Batfish vehicle measuring physical and biological parameters consisting of chlorophyll *a*, zooplankton, conductivity, temperature, and depth. Continuous profiling (~30 h) through the boundary zone revealed intrusions at the subsurface front consisting of plumes of ascending slope water overlying descending surface coastal water both moving vertically and horizontally. Movements of the intrusions were coherent with M_2 tidal cycles and exhibited localized turbulent mixing ascribed to shear instabilities. This mixing gives rise to a potentially efficient mechanism for vertical transport of heat and salt particularly as input to the Scotian Shelf. These intrusions also form inversion layers consistent with earlier observations which showed that these layers can decay over longer time scales by double diffusion processes. The vertical mixing at the subsurface front may also account for the anomalously high productivity along the front by means of continual replenishment of nutrients from below.

Key words: physical oceanography, biological oceanography, Scotian Shelf, profiling

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On s'est servi d'un véhicule «Batfish» capable de mesurer les paramètres physiques et biologiques suivants : chlorophylle *a*, zooplancton, conductivité, température et profondeur pour établir un profil détaillé de la frontière eau de plateau/eau de pente au sud de la Nouvelle-Ecosse. Des profils continus (~30 h) dans la zone frontalière révèlent des intrusions au front en sous-surface, constituées par des panaches d'eau de pente ascendante recouvrant l'eau côtière superficielle descendante, les deux se déplaçant verticalement et horizontalement. Les mouvements des intrusions sont en accord avec le cycle des marées M_2 et montrent le mélange turbulent localisé imputé à des instabilités causées par cisaillement. Ce mélange donne naissance à un mécanisme potentiellement efficace de transport vertical de chaleur et de sel, particulièrement vers le plateau continental Scotian. En outre, ces intrusions sont à l'origine d'inversions s'accordant avec observations antérieures qui ont démontré que ces couches, par des processus de double diffusion, peuvent prendre plus de temps à se décomposer. Le mélange vertical au front de la sous-surface peut aussi expliquer la productivité exceptionnelement élevée le long du front par renouvellement continu d'éléments nutritifs provenant des couches inférieures.

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THE sharp boundary zones separating coastal and warmer slope water are characteristic of the shelf break region off Nova Scotia and such zones are thought to be sites for convergence of surface water masses (Okubo 1977) as well as high productivity. For the most part, these fronts outcrop at the surface and during the spring bloom period become a region of highly localized aggregations of phytoplankton represented by concentrations that are higher than in nearby shelf or slope waters (Fournier et al. 1977, 1979). Such regions of productivity enhancement in the British Isles have been also reported by Pingree et al. (1975) and Savidge (1976) and one explanation for high productivity in frontal zones has been suggested by Simpson and Pingree (1977). In these regions, dense phytoplankton blooms persist in the surface layers on the stratified side of the frontal boundary where light levels are high but nutrients have been originally depleted as a result of spring blooms. On the unstratified side, strong tidal stirring provides complete vertical mixing (Pingree et al. 1975) such that high nutrient concentrations near

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the bottom are mixed uniformly through the water column. However, the intensity of mixing there and lack of stratification precludes the phytoplankton spending most of their time at high light levels with the accompanying enhanced production. The front provides an interface for mixing whereby nutrients in the well mixed waters are continuously transported approximately horizontally into the stratified waters where the phytoplankton can utilize them while the stratification prevents them from sinking rapidly to lower light levels. Simpson and Pingree (1977) observed such conditions to persist through the summer months. In our shelf break region the source of enhancement is evidently the nutrient-rich slope waters (Fournier et al. 1977) which also appears to be the important source of enrichment for the Scotian Shelf (Smith et al. 1978). Vertical transport of nutrients is required in order to explain the high productivity at the frontal boundary and in the warmer slope waters but the underlying mechanisms are not well understood. Voorhis et al. (1976) and Horne (1978) observed interleaving layers at frontal boundaries and produced flux estimates based on small scale mixing processes such as double diffusion.

The purpose of this paper is to describe the experimental results obtained by rapid and high resolution profiling of physical and biological parameters at the frontal region using a Batfish and to offer some interpretation of these results indicating vertical mixing processes at the subsurface front. First, profiles of temperature, salinity, density, and chlorophyll contoured against depth from 10 to 100 m are presented for an onshore–offshore transect traversing the front. The influence of the M_2 semidiurnal tidal constituent (onshore–offshore) is resolved and is represented by the physical movements of the chlorophyll layer in the front. Then a time sequence of the frontal movements is presented revealing a bimodal plume whose vertical movements are coherent with M_2 tidal oscillations and consists of ascending slope water and descending surface coastal water intruding at the subsurface front. Estimates of mixing enhancement from turbulent shear instabilities are made and brief discussion is presented on double diffusion processes. Finally, an explanation is presented for the high productivity and hence high concentrations of phytoplankton within the front in terms of nutrient replenishment.

Experiment and Instrumentation

The operational area is shown in Fig. 1 illustrating the approximate location of the frontal boundary ~100–200 miles south of Nova Scotia. The contour of the frontal boundary in Fig. 1 was the result of a smoothed average of two (weekly) satellite (IR) photographs (issued by the U.S. Naval Oceanographic Office) chosen for coverage during our operational period (April 29–May 9, 1977). The surface front was defined by an approximate temperature contrast of ~6–12°C. The satellite photograph of May 11, 1977 showed the warm-core eddy moving north and drawing coastal water from the northwest at ~42°00′N. On May

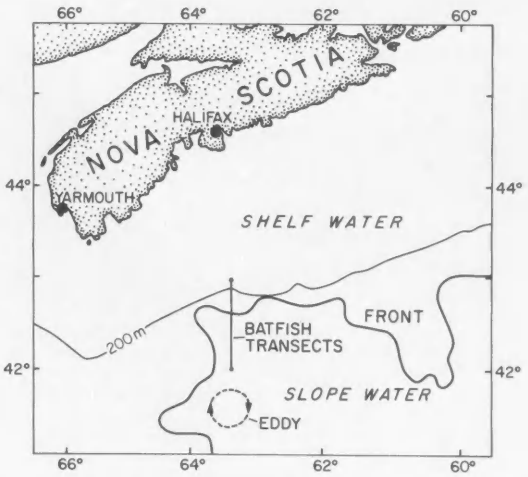

FIG. 1. Scotian Shelf and slope water region. The mean position of a thermal front with surface temperatures of ~9–11°C was contoured from satellite imagery and partly from Batfish profiling. The work area for Batfish transects is shown along 63°25′W.

7 and 8, Batfish tows were made northwards starting from 43°00′N and 42°30′N, respectively, along the transect (63°25′W) and the presence of slope water only (and not the eddy) was indicated south of ~42°30′N. Therefore the eddy and the associated movement of surface coastal water did not occur until after our operational period and subsequent to this, during the following week, the western frontal boundary moved eastward to ~63°00′W.

The indicated transect situated along 63°25′W and bounded by 42° to 43°N was sampled continuously during the period of April 29 to May 9, 1977. The north–south line was chosen to lie near a line of current meter moorings along 63°30′W as part of the Shelf Break Mooring Program organized by the Bedford Institute of Oceanography (Smith and Petrie 1976) and provided an excellent physical picture of water movements in our sampling area. The cruise (#77007) was a multidisciplinary program consisting of the Atlantic Oceanographic and Marine Ecology Laboratories at the Bedford Institute of Oceanography and was designed to study intensively the small-scale physical events and the biology of the shelf and slope water boundary zone.

High resolution and rapid profiling of the front was accomplished by towing a cycling Batfish vehicle equipped with the following sensors: (1) a digital CTD unit (prototype to the Model 8700 series, Guildline Instruments, Smith Falls, Canada); (2) a modified in situ Variosens fluorometer (Impulsphysik, GmbH, Hamburg, West Germany); and (3) an in situ electronic zooplankton counter (prototype unit). The conductivity, temperature, and depth sensors have accuracy specifications of ±0.01‰, ±0.01°C, and ±1 dbar (full-scale 0–400 dbar), respectively, and resolution specifications of ±0.005‰, ±0.003°C, and ±0.2 dbar, respectively. Midway through the cruise period, some spikes of short duration (100–200 ms) on the conductivity signal due to a faulty underwater connector were observed; however, these were removed and digitally filtered by computer

software. Wherever applicable, these errors will be quoted or discussed.

The Variosens fluorometer is used to measure chlorophyll *a*, the estimator of standing crop of phytoplankton, and is capable of detecting levels of ~0.3–30 mg·m^{-3} in an error range of ~3–15% depending on concentration. The fluorometer towed on Batfish is able to resolve spatially ~3 m in the horizontal and ~0.5 m in the vertical scales at a towing speed of 3 m·s^{-1}. The horizontal resolution of each vertical (actually oblique) profile made by the Batfish is ~0.6 km or ~1.2 km per cycle which should be sufficient to resolve the dominant phytoplankton patch scales thought to be in the range of 5–10 km (Denman et al. 1977). A detailed description of the system has been presented elsewhere (Herman and Denman 1976). An example of its resolution and profiling capabilities for physical and chlorophyll structure is found in studies conducted in a local upwelling region off Yarmouth, Nova Scotia, as described by Denman and Herman (1978).

The in situ electronic zooplankton counter is used for the counting and sizing of zooplankters in the size range of ~0.4–4 mm and the complete system mounted on Batfish has been described in detail by Herman (1977), Dauphinee (1977), and Herman and Dauphinee (1979). A detailed analysis of zooplankton distributions in and near the front is beyond the scope of this paper; however, some of the general features of this data are discussed briefly to provide supporting background. Zooplankton data, fluorescence, conductivity, temperature, and depth are digitally transmitted (10 s^{-1} for CTD and fluorometer data) to a HP 2100 minicomputer for on-line plotting and data storage on magnetic tape.

The Batfish (Dessureault 1976) is a towed streamlined body designed specifically for transporting oceanographic sensors and is capable of cycling between two depths to maximum of 400 m. The tested maximum for biological profiling is ~250 m. Towing rates are 3 m·s^{-1} and diving rates are present to 0.5 m·s^{-1}.

Profiles and Characteristics of the Frontal Region

Contoured profiles of temperature, salinity, density, and chlorophyll *a* on depth (10–100 m) traced by the Batfish are presented in Fig. 2 for the north-south transect bounded by 42°30′ to 43°00′W (refer to Fig. 1) and encompassing both the slope and coastal waters. Slope water can be identified (McLellan 1957; Fournier et al. 1979) by its T–S characteristics and south of the front temperature was measured in the range from ~10–13°C and salinity ~34.5–35.0‰. The frontal boundary was characterized in the surface layer by a high horizontal temperature contrast ranging from ~7 to 11°C and gradient ~0.5°C·km^{-1} and salinity contrast ranging from ~32.5 to 34.5‰ and gradient ~0.2‰·km^{-1}.

In coastal water along the transect, chlorophyll concentrations were generally low (~1–2 mg·m^{-3}) and were measured over depths from surface to ~40 m. In slope waters, the chlorophyll levels were higher (2–3 mg·m^{-3}) and varied greatly over the upper ~70 m. The highest values were measured in the front itself and

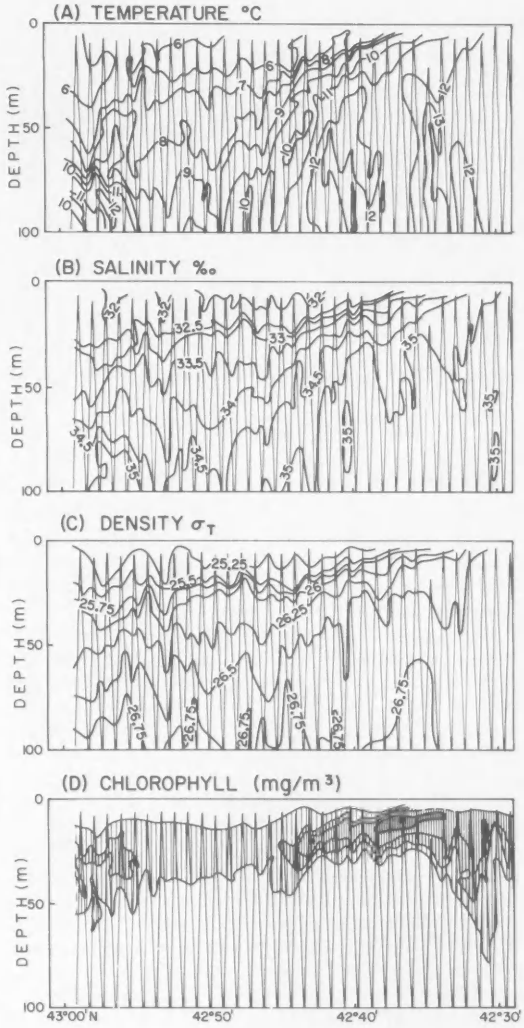

FIG. 2. Contoured profiles of (A) temperature, (B) salinity, (C) density, and (D) chlorophyll *a* on depth (10–100 m) between 42°30′N and 43°00′N. Increased shading indicates concentrations ranging from 1 to 5 mg·m^{-3}.

ranged from 4 to 5 mg·m^{-3} with localized peaks sometimes measured at ~6–7 mg·m^{-3}. Chlorophyll was distributed obliquely along the frontal boundary extending ~10 km in the horizontal and from surface to ~40 m in the vertical direction and was coherent with temperature and density patterns. By sampling frequently (~daily) using both the Batfish and pumped samples it was found that these chlorophyll levels persisted (constant to ~±20%) throughout the cruise period within the front, in slope, and coastal waters.

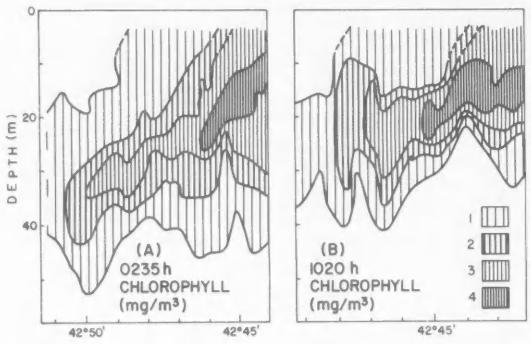

FIG. 3. Two examples of vertical orientation of the frontal chlorophyll layer illustrating (A) the lowered position, and (B) the raised position.

M_2 Tidal Variations and Frontal Characteristics

The Batfish tow illustrated in Fig. 2 was designed to show broad features and variations between coastal and slope water. Effort was then focused in the boundary zone and the front was profiled continuously along a 20 nautical mile transect bounded by 42°40′ to 43°00′N seven times in a period of ~24 h. Each transect was a reverse course of the previous one requiring ~3–4 h of towing and occasional equipment recoveries and maintenance. Variation in properties were evident; however, the most systematic variations were observed in the horizontal and vertical movements of the chlorophyll layer. An example of two cases is given in Fig. 3A and B. Here the mean vertical motion was observed from the mean vertical change (~10–20 m) of the contours (e.g. 2 mg·m^{-3}) in the tail (lower half) of the chlorophyll layer. Changes in the frontal chlorophyll layer that took place during the 3–4 h of each tow were not resolvable, that is, each transect was not a frozen "snapshot" on time scales associated with the M_2 tidal influence. The gross features of the layer, however, appeared reasonably uniform for each two. For example, the layer thickness (~15 m bounded by the 2 mg·m^{-3} contour) was nearly constant, the length (~12 km) was reasonably constant (defined by the 2 mg·m^{-3} contour on the north end and by the projected outcropping on the south end) and the maximum chlorophyll concentrations remained constant to within ±20%. The movements of the chlorophyll layer were quantified by evaluating the centroid of its depth $\bar{D}$, and position $\bar{X}$, along the transect from the equations

$$(1)\quad \bar{D} = \sum_j \sum_t D_{jt} C_{jt} / \sum_j \sum_t C_{jt}$$

and

$$(2)\quad \bar{X} = \sum_j \sum_k X_{jk} C_{jk} / \sum_j \sum_k C_{jk}$$

where C, D, X are the chlorophyll values, depths, and positions along the transect evaluated for the j^{th} profile,

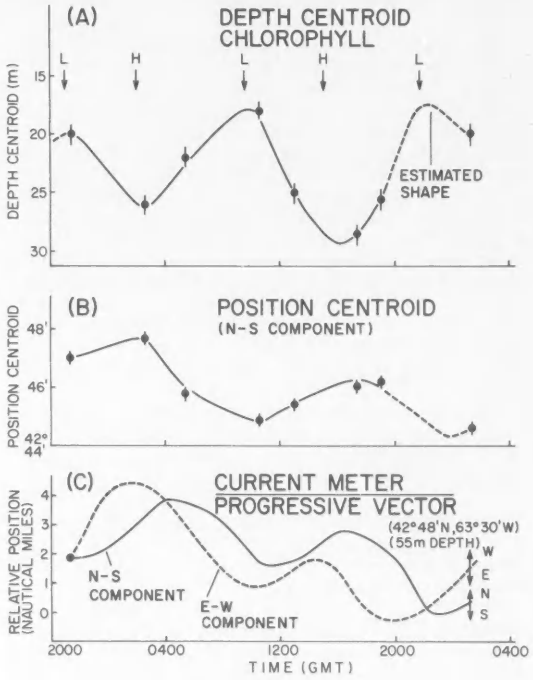

FIG. 4. M_2 tidal variations of the chlorophyll layer as characterized by (A) its depth centroid, and (B) its position centroid. The tidal nodes are indicated by L, H (Low and High) in Fig. 4A. Figure 4C represents the north–south and east–west component of the progressive vector of a current meter located at 42°48′N, 63°30′W, and at ~55 m depth.

i^{th} depth, and k^{th} position. Equations 1 and 2 were evaluated for the case of the chlorophyll layer bounded by an imaginary box ~12 km long and for chlorophyll levels chosen such that $C > 1.5$ mg·m^{-3}. The northern side of the box left-hand side of Fig. 2a and b was systematically located at the 2 mg·m^{-3} chlorophyll contour. The centroids for depth and position are plotted in Fig. 4A and B against time of day (arrival time at the centroid) for the period commencing at 2130 h (GMT), May 7, to ~0120 h, May 9. The estimated cyclic variation of the depth centroid in Fig. 4a shows a periodicity of ~12 h and demonstrates the resolution of the M_2 tidal constituent. The semidiurnal tidal nodes indicated by arrows above the plot were taken from tidal tables for Halifax and show reasonable agreement with the estimated nodes of the depth centroids. The north–south movement of the layer along the transect is also represented by its position centroid plotted against time in Fig. 4B. The cyclic variation of position may be compared to the north–south component of the progressive current vector (shown in Fig. 4C) evaluated from current meter data at 63°30′W, 42°48′N

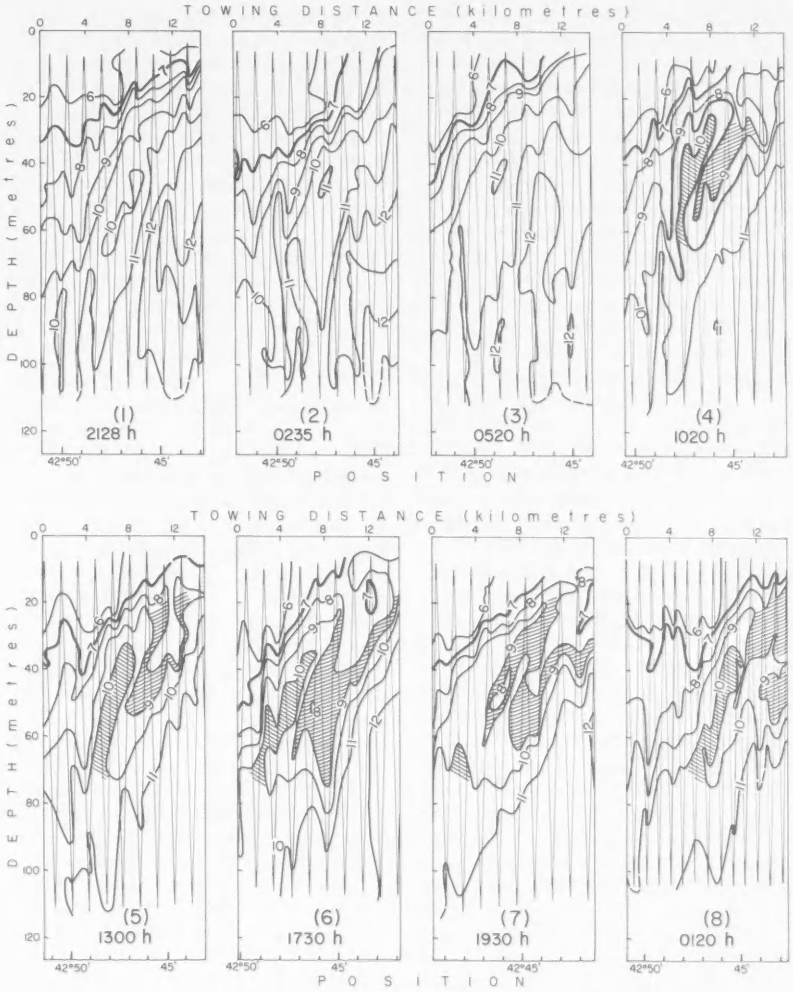

FIG. 5. Time sequence of temperature profiles of the front taken by Batfish over a period of ~30 h. A bimodal intrusion is seen to occur in panel 4 (enhanced by dark lines).

at a depth of 55 m and indicates marked similarity. Although the net movement of the front during spring is northward towards the shelf break, there are fluctuations such as net southward drift shown in Fig. 4C which lasted ~1 wk.

The same cyclic variations were observed for the depth centroids of a zooplankton layer (~15 m thick) measured at the front and were situated ~5 m above the centroids of the chlorophyll layer and moved coherently with the layer. Since there was E–W advection over the sampling period, it would appear that the observed correlation of the zooplankton depth centroids with the density (or cholrophyll) front was a feature that existed alongshore to some extent in our sampling area. However, the effects of vertical shear above the front on the spatial distribution of zooplankton and their response to these effects is not known. There was no apparent migration of the zooplankton downwards through the chlorophyll layer over the 30 h sampling period nor was this observed in any other profiles taken throughout the cruise.

The time sequence of the thermal front is shown in Fig. 5 for a total of eight transects (including that of Fig. 2) depicting the movements coherent with the semidiurnal tidal cycles. The times indicated on each panel are the arrival times at the chlorophyll centroids of Fig. 4 and the positions of the panels are not fixed but selected to accommodate the north–south move-

ment of the front as well as depicting its most salient features. Panels 1 to 2 of Fig. 5 indicate a net "lowering" in the upper 30 m of the front as depicted by the 7° isotherm, for example, followed by a net "lifting" seen in panels 2 to 3. In panel 4, the front appears in its highest position corresponding to the measured tidal node in Fig. 4. There also appears in panel 4 a bimodal intrusion consisting of a 9°C plume of water apparently descending from surface and a 10°C plume of water ascending from slope water. In the remaining panels, the frontal movements were also coherent with the tidal cycles. The 10° plume appeared to recede in panels 5 to 6, disappeared in panel 7, and reappeared in panel 8 approximately 3 h following another M_2 tidal low. The descending plume in panels 5 to 8, however, did not follow the tidal movements but appeared to enlarge as indicated by the 9° isotherm. For the most part, the movements of the slope water plume were coherent with M_2 tidal cycles; however, this is not a continuous feature since it did not manifest itself earlier in panel 1. This was also borne out by earlier Batfish profiles made throughout the cruise indicating that these intrusions were present at the subsurface front ~40% of the time.

The data presented in Fig. 4 and 5 can be compared to tidal data obtained for the Scotian Shelf and Slope by Petrie (1975). He showed from tidal analysis that oscillations at semidiurnal periods were primarily the M_2 constituent and that on the slope there was a strong internal tide in addition to the barotropic component. The oscillations of the depth centroid in Fig. 4A describe vertical excursions in the surface layer (~30 m depth) of ~8–10 m peak to peak. These excursions are considerably larger (~×10) than those measured for surface tides and therefore must be characteristic of internal tides. The estimates of vertical excursions are highly variable, of course, since the centroid represents a mean position in the layer and there exists larger (or lesser) local excursions, for example, of ~±10 m the lower end of the chlorophyll layer. Horizontal tidal flow was estimated from the position centroids of Fig. 4B at ~27 cm·s^{-1}. This latter estimate is ~8 times larger than the M_2 barotropic component of horizontal flow (~3.5 cm·s^{-1}) estimated at the slope by Petrie (1975) and therefore further indicates the presence of strong internal tides. The internal tides are also phase locked to the surface tides as indicated by the correlation between the centroid tidal nodes and the Halifax tidal peaks.

Petrie (1975) also presented evidence indicating that internal wave activity of tidal frequency could be generated between a sloping bottom and the surface tides. The wave would be propagated upwards towards the surface and could be refracted in the direction of a sloping density surface such as the front. It is possible that the bimodal plume of Fig. 5 could be described by such an internal wave.

Mixing at the Subsurface Front

The observations made thus far neglect the influence of the alongshore component of advection in the east-west direction during the sampling period. The alongshore variability through our specific sampling area was known from current meter data obtained at 55 m depth at the subsurface front and is shown in Fig. 4C. Note that the east–west advection (derived from the progressive vector) from panels 1 to panels 4 and 5 (of Fig. 5) was nearly zero indicating there was not net movement of water mass along this component. The inference can thus be made, with caution, that to the extent that current meter measurements at 63°30′W were representative of currents along 63°25′W where the Batfish transects were made, then the plume structure that developed between panels 1 and 5 of Fig. 5 did not result from alongshore advection.

Therefore if we assume that the plumes were a result of vertical motion (and not E–W advection) and were moving in opposite directions in the horizontal then a crude estimate of possible turbulent mixing by means of Kelvin–Helmholtz instabilities can be made from vertical shear estimates at their interface. Both plumes shown in panel 4 (Fig. 5) have approximate horizontal scales of ~5 km and mean amplitudes of ~15 m. If the horizontal distance were traversed in a period of ~5 h, that is, the time difference from panel 3 where there was no apparent plume, to panel 4 where it appeared, then for a vertical shear estimate of $\partial V/\partial Z \simeq 0.04\ s^{-1}$, the Richardson number can be evaluated from

$$(3)\quad J = (g/\rho)(\partial\rho/\partial Z)/(\partial V/\partial Z)^2 \simeq 0.4\ {}^{+\,0.6}_{-\,0.2}$$

A condition for turbulence requires that the average $J < 0.25$. It is improbable that the entire plume was turbulent; however, on the basis of an average value of $J \simeq 0.4$ it is not unreasonable to expect localized values <0.4 and therefore to expect spatially localized turbulent mixing. Although the expected localized turbulence would be on a much smaller spatial scale than that of the plumes, the exact spatial scales, distribution and frequency cannot be determined from the picture presented here. Such estimates are intended as an indicator only, and the possibility of turbulent mixing requires further examination of the physical characteristics of the plumes.

T–S and σ_t Profiles

Two T–S profiles (Batfish cycle) of the central region of the plumes (~8 km mark of panel 4, Fig. 5) are illustrated in Fig. 6. The left and right halves of the plot conform to the T–S characteristics of coastal water and slope water, respectively. The region between the vertical bars was mixed water (without invoking the mixing mechanism here) and is generally thought to have as its constituents coastal and slope water (Fournier et al. 1979). The mixed region shows the temperature inversion measured in the plumes but also indicates a salinity inversion of ~0.2 (±0.03) ‰. Here there existed a warm salty layer overlying a cool fresh

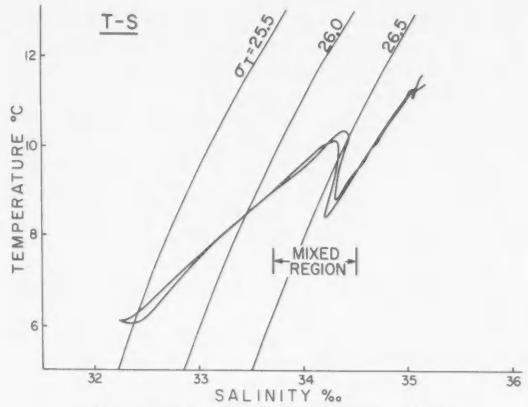

FIG. 6. T–S profiles of the plume region.

layer and is consistent with the picture of ascending slope water overlying descending coastal water.

Contours of σ_t in the same region of the plumes of panel 4 are shown in Fig. 7A (indicated by the dashed lines) and are contrasted against temperature contours of the plumes (indicated by solid lines). A descending series of density "troughs" in succession are seen in the region of the 9°C plume and are most probably attributable to instrumental sources. High vertical temperature gradients existing within the plume could result in a mismatch in phase of the temperature and conductivity sensors and it is estimated that the best possible density resolution obtained in this region was $\Delta\sigma_t \leq 0.05$. Therefore the only qualitative conclusion that may be drawn from these data is that the density structure within the plume (between $\sigma_t = 26.5$ and 26.75) is consistent with the localized vertical density gradients rapidly becoming small. This is also consistent with the Richardson number $J \to 0$ in Eq. 3, a required condition for turbulence.

In addition to instrumental uncertainties, the density "troughs" (and short wavelength T and S fluctuations in Fig. 5 and chlorophyll fluctuations in Fig. 8) could be caused by internal waves with wavelengths too short to be resolved. In the eastern Gulf of Maine near Yarmouth, Nova Scotia, we (Denman and Herman 1978) found short internal waves to have such large amplitudes that mesoscale features became evident only when the sections were plotted against σ_t rather than depth. However, for the sections presented here, patterns on scales similar to the width of the front (3–10 km) were obvious without resorting to plots against σ_t. Hence, we conclude that internal waves on scales less than or equal to the Batfish cycling distance had amplitudes small compared to that of the plume structure.

The plumes themselves appear to have been moving along isopycnal surfaces as in the case of the 9°C plume where it is bounded by $\sigma_t \simeq 26.5$ to 26.75 and similarly for the 10° plume which perhaps shows a small isopycnal crossing of $\Delta\sigma_t \simeq 0.3$ at $\sigma_t \simeq 26.5$. This corresponds to the more classical picture of mixing along an isopycnal surface thereby minimizing the kinetic energy requirements for vertical movement of the plumes.

Figure 7B shows the density structure of the front during high tide, that is, for the case of panel 2, Fig. 5. By comparison to Fig. 7A it is seen that the isopycnal surfaces in the surface layer ($\leq$30 m) are raised during low tide and are more inclined in the horizontal. This is consistent with the earlier observation of the "raised" position of the chlorophyll layer during low tide.

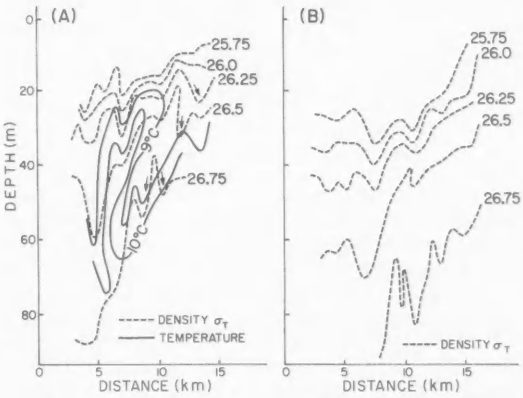

FIG. 7. (A) Isopycnal surfaces (dashed lines) contrasted by temperature (solid lines) for the plume region and illustrating a sharp decrease (arrows) in vertical density gradient; (B) Isopycnal surfaces before the onset of the plumes.

Phytoplankton Dispersion at the Front

A localized anomalous decrease in chlorophyll within the frontal layer was observed in the surface region (0–20 m) directly above the intrusions illustrated, for example in Fig. 8B. The decrease implied that there was a dispersion of phytoplankton cells (defined here as the dispersal of phytoplankton cells into a larger water volume) at this locale which was caused by one or a combination of two possibilities: (1) physical advection of cells (probably downward) by the coastal water plume, or (2) east–west advection. Both of these possibilities will be discussed here.

Figure 8 illustrates a "before and after" situation whereby the chlorophyll layers situated above the plume were contoured for panels 3, 6, 7 of Fig. 5. Figure 8A shows the physical structure of the chlorophyll layer within the front prior to the intrusions. Figure 8B and C show the state of the layer ~7–10 h following the onset of the intrusions and were chosen from the available data to illustrate the most pronounced decrease in chlorophyll over the plume region. This effect was also observed for the zooplankton layer situated just above the chlorophyll layer in Fig. 8 where the measured

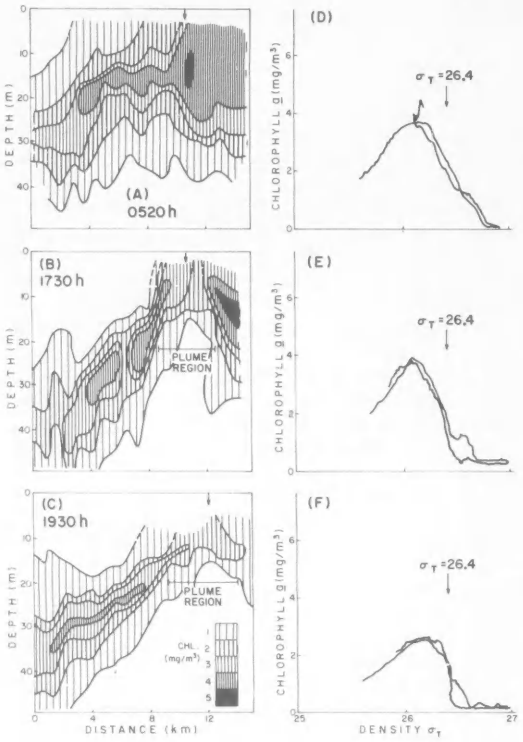

FIG. 8. (A) Frontal chlorophyll layer before the plume, and (B, C) the layer showing an anomalous decrease in chlorophyll in the plume region; (D, E, F) illustrate the chlorophyll versus σ_t relationship corresponding to (A, B, C), respectively.

zooplankton concentration decreased by a factor of ~15 in the region over the plume.

The relationship of chlorophyll to density σ_t was also examined for each case of Fig. 8A, B, C at positions indicated by arrows and plotted in Fig. 8D, E, F for two vertical profiles. Figure 8D illustrates the C versus σ_t relationship for profiles prior to the intrusions and demonstrates a linear relationship in the region below the chlorophyll maximum, that is, for $26.2 < \sigma_t < 26.8$. The second profile of Fig. 8D peaks at $C \simeq 4$ mg·m^{-3} and $\sigma_t \simeq 26.0$ and corresponds to the contours breaking near surface in Fig. 8A. In Fig. 8E and F it is seen that the chlorophyll levels are lower and rapidly decrease at $\sigma_t \geq 26.4$ where there is no systematic dependence on σ_t observed. At $\sigma_t \simeq 26.4$, the chlorophyll gradient is extremely high (particularly in Fig. 8F) and indicates short term instabilities (consistent with mixing) occurred just below the frontal chlorophyll maximum and in a region over the plume. These large gradients were measured at all stages of the intrusions (i.e. panels 4 to 7); however, the anomalous decrease was most pronounced at ~7 h (Fig. 8B) following the onset of the intrusions. If the coastal water plume was physically advecting phytoplankton cells downward then the decrease should have occurred simultaneously with the beginning of the intrusions. We may in fact have observed some easterly component of the intrusions along the front being advected past our sampling transect. This is consistent with the progressive current vector of Fig. 4C indicating a net eastward advection of ≃1–2 miles during the period corresponding to Fig. 8B and C or ~7–10 h following the onset of the intrusions. In this latter period the downward plume appears thermally enlarged (panels 5 to 8, Fig. 5) indicating the possibility of larger scale mixing and therefore a more pronounced decrease in chlorophyll over the plume.

This interpretation is difficult to resolve further; however, the data of Fig. 8 qualitatively demonstrates two points: (1) there is a significant decrease in chlorophyll occurring over the plume, and (2) the chlorophyll-σ_t relationship existing before the intrusions breaks down afterwards (notably below the chlorophyll maximum) indicating processes consistent with mixing and cell dispersion.

Discussion

The intrusion processes proposed here are not inconsistent with the double diffusion processes proposed by Voorhis et al. (1976) and Horne (1978) but in fact may be their source mechanism. The end result of the intrusions was to form a layer of warm salty water overlying a layer of cool fresh water and these layers could have continued to decay by double diffusion thus adding further to heat and salt exchange at the subsurface front. The proposed lifetime of the inversion layer depicted in Fig. 6 was estimated at ~21 h in agreement with Horne's estimates of ~31 h. However, the inversion layer measured here could not be further analyzed for its decay on the estimated double diffusive time scale due to the additional complication of the apparent cooling of the coastal water plume.

The nature of the mixing processes essential to high productivity at fronts in the English Channel and Celtic and Irish seas have been studied extensively by Pingree et al. (1975) and Simpson and Pingree (1977) and the biological characteristics of these fronts are somewhat similar to observed properties of the Scotian Shelf break front. In the fronts of the British Isles, the source of vertical nutrient transport is tidal stirring and the nutrient levels below the front were extremely high, for example, nitrates ranging from ~2 to 7 mg at·m^{-3}. Above the front, biomass was high (chlorophyll concentrations ranging from ~5 to 100 mg at·m^{-3}) and light levels were favorable for phytoplankton growth. In the latter case, the nutrient levels were low (<1 mg at·m^{-3}) a condition resulting from the spring bloom. The combination of regimes therefore were suitable for rapid and sustained phytoplankton growth which was

observed to persist throughout the summer months. The higher cell concentrations in the thermocline and the persistence of the chlorophyll maximum reflected the reduced tendency for dispersal by turbulence. Also the cells in this region were the first in line for nutrients.

The biological structure measured here in the frontal region of the Scotian Shelf break bears somewhat similar characteristics. The source of vertical nutrient transport is not tidal stirring but is proposed to be intermittent tidal intrusions. The nutrient levels below the front in slope water were high with nitrate concentrations >4 mg at$\cdot$m^{-3} (Irwin et al. 1978). Nitrate concentrations above the front were low at ~ 0.4 mg at$\cdot$m^{-3} (nutrient depleted as a result of spring bloom), however, concentrations within the front itself or equivalently within the chlorophyll maximum were intermediate at ~ 2 mg at$\cdot^{-3}$. This may indicate that nutrient depletion within the front was somewhat offset by nutrient replenishment due to underlying vertical mixing. The chlorophyll layer existing at the front appeared discretely cut-off from the lower layer, and this may also have been reflected in the tendency for cell dispersal by turbulence. This process may have also been operating on the zooplankton which were found in high concentrations above the thermocline.

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Aggregation, Transformation, and the Design of Benthos Sampling Programs[1]

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DOWNING, J. A. 1979. Aggregation, transformation, and the design of benthos sampling programs. J. Fish. Res. Board Can. 36: 1454–1463.

Solutions are offered to the problems of data transformation and the design of efficient programs for sampling the benthos of lakes and large rivers. All types of benthic animals from many types of substrate, sampled with diverse sampling gear, are aggregated in a similar fashion. Aggregation can be indexed by the unbiased exponent of the power relationship between density and variance. A single variance stabilizing transformation can be used for all macrobenthos population data since the relationship of sample variance to mean density is similar in all taxa of benthic animals. Stabilized variance in population data satisfies one of the main assumptions of the analysis of variance and allows use of normal statistics provided that the other assumptions are met. The fourth-root transformation stabilized the variance in all macrobenthos samples while either the commonly used square root or logarithmic transformations did not. Sampling programs can be optimized empirically. Standard deviation (s) is predictable from mean density (M; m^{-2}) and sampler size (A; cm^2) from the equation: $\log_{10}s = 0.581 + 0.696 \log_{10}M - 2.82 \times 10^{-4}A$. The data show that it is easier to obtain a precise estimate of macrobenthos density at high densities. Small diameter samplers are most efficient in obtaining high levels of precision. Data were taken from the literature.

Key words: aggregation, benthos, freshwater, regression, sampling, transformation

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L'auteur offre des solutions aux problèmes de transformation des données et conception de programmes efficaces d'échantillonnage du benthos de lacs et de grandes rivières. Tous les types d'animaux benthiques habitant divers types de substrats, échantillonnés à l'aide d'engins différents, sont groupés de la même façon. Un indice d'agrégation peut être déduit d'un exposant non biaisé de la relation géométrique entre densité et variance. On peut utiliser une seule variance stabilisant la transformation pour toutes les données sur les populations macrobenthiques, puisque la relation entre variance d'échantillonnage et densité moyenne est semblable dans tous les taxons d'animaux benthiques. La variance stabilisée dans les données sur les populations est conforme à l'une des principales hypothèses d'analyse de variance et permet l'emploi de statistiques normales, pourvu que l'on se conforme aux autres hypothèses. La transformation à la quatrième racine a pour effet de stabiliser la variance dans tous les échantillons de macrobenthos, alors que ce n'est pas le cas pour les transformations en racines carrées ou logarithmiques communément utilisées. On peut optimiser empiriquement les programmes d'échantillonnage. Il est possible de prédire l'écart type (s) à partir de la densité moyenne (M; m^{-2}) et la taille de l'appareil d'échantillonnage (A; cm^2) à partir de l'équation : $\log_{10}s = 0{,}581 + 0{,}696 \log_{10}M - 2{,}82 \times 10^{-4}A$. Les données démontrent qu'on obtient plus facilement une estimation de la densité du macrobenthos à de hautes densités. Des appareils d'échantillonnage de faible diamètre permettent d'atteindre de plus hauts niveaux de précision. Les données ont été extraites de travaux publiés.

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BENTHIC population estimates made in lakes and large rivers are highly variable. This is due to their distribution which is usually aggregated or contagious (Elliott 1977). Analysis of data and the design of sampling surveys for aggregated populations are difficult, yet are of great importance if we wish to make precise estimates of benthic populations. The problems involved in making biomass estimates of benthic animals are even more difficult since precise estimates of both population and weight must be made. In this paper I offer solutions to the problems of aggregation, treatment of data, and the design of sampling surveys, towards the precise estimation of benthos population density.

Many measurements of the aggregation of organisms in space have been proposed (e.g. Elliott 1977; Southwood 1966; Paloheimo and Vukov 1976). Indices of aggregation fall into two categories: those

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that can be derived from population estimates from sets of randomly placed samples, and those that must be derived from measures of distance between individuals. Although indices based on the spacing of individuals are the best measures of aggregation (Paloheimo and Vukov 1976), these indices will not be discussed here because they are impossible to apply to small animals which cannot be observed directly. Only the indices calculable from distributions of population estimates such as those collected by grabs and corers will be considered here. In this paper I apply one of these indices to a large body of benthic data to examine the tendency of organisms to aggregate.

The amount of clumping that we find will dictate the method of data analysis. Since benthic population estimates are usually found to be contagious, the distribution of density estimates of any particular population will be nonnormal and nonrandom. Aggregated data require the use of nonparametric statistical techniques or data transformation prior to parametric statistical analysis. Easy-to-use nonparametric techniques (Conover 1971) should be used for hypothesis testing in situations where data cannot be made to conform to the assumptions of analysis of variance. In many cases, the use of statistical methods based on the normal distribution is more desirable because these methods are useful in summarizing the structure underlying a body of data (Andrews et al. 1971). I will discuss only the transformation of data toward the use of parametric statistics because parametric techniques are widely available and understood, are dominant in computer packages of statistical programs, and are simple to compute.

The second section of this article is a guide to the researcher in the design of sampling programs. The conclusions were derived from published benthic data. This paper suggests ways in which more interpretable data can be collected and ways of interpreting benthos data more precisely.

Data and Analysis

The data used in this analysis were collected from published literature as well as government reports. A survey was made of the articles listed in *Biological Abstracts* for the years 1968–78 (Index: benthic, benthos, bottom, macrobenthos, sediment). Over 600 abstracts were screened in this manner from which 260 papers were examined. A computer literature survey done by the New England River Basins Commission (Key words: benthos, benthic, macrobenthos, and related terms) yielded 1126 abstracts and many sets of data. While many of the papers promised "quantitative" data, only 23 papers yielded data for the data set because many authors reported only mean densities and no measure of dispersion.

The data set derived from the literature consists of measures of mean density ($\bar{x}$) and variance (s^2) for various taxa and groups of taxa; also included are sampler type, sampler size, number of replicates, and sediment type. Nearly all of the data were counts of animals retained on a 500–600 μm mesh. Some samples (52 sets out of 1462) were obtained using a 270–350 μm mesh. These samples did not perform differently than those sieved with larger screens. Data from studies in which subsampling occurred were rare and were not included. The data are available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2. I also have a computer tape available for those wishing to perform further analysis.

The data set discussed here contains estimates of benthic populations and dispersion from many countries around the world. No data were rejected on grounds other than lack of true replication (i.e. replicates all taken same time, same station, same sampler). The data set was constructed primarily for examination of the freshwater benthos of lakes, ponds, and large rivers.

Regression analysis is used to fit linear functions to sets of data points throughout this paper. Although both variables were subject to error, linear regression analysis was performed using the Model I or least-squares method ($b = \Sigma xy/\Sigma x^2$). Model I regression was used instead of the computationally complex Model II (Sokal and Rohlf 1969) analysis because of the large amount of data processed. Model II regressions were also performed on subsets of the data using Bartlett's three-group method (Sokal and Rohlf 1969); slopes, intercepts, and confidence intervals of slopes were very similar to those found using Model I techniques (Table 1). The similarity of estimates by both techniques is due to large sample sizes and high correlations between variables (Ricker 1973).

TABLE 1. Comparison of Model I (least squares) and Model II (Bartlett's three group method — Sokal and Rohlf 1969) techniques for the estimation of slopes (b) and confidence intervals of slopes (95% C.I.) for log–log regressions of s^2 on the $\bar{x}$ of replicate benthos samples. n indicates the number of sets of data used in the analysis and r^2 is the coefficient of determination (Steel and Torrie 1960). The data indicate that there is little difference between the results of the two methods of estimation.

			Model I		Model II	
Taxon	n	r^2	b	95% C.I.	b	95% C.I.
Acari	22	0.98	1.71	1.59–1.83	1.68	1.52–1.83
Hirudinae	34	0.54	1.04	0.70–1.39	1.03	0.59–1.46
Nematoda	24	0.88	1.78	1.49–2.07	1.66	1.37–1.86
Platyhelminthes	34	0.87	1.56	1.34–1.77	1.43	1.14–1.68

Aggregation and Transformation

Aggregation

Not only is the aggregation of organisms of interest to ecologists from a behavioral standpoint, but to analyze population data properly it is also necesary to measure the degree of aggregation accurately. Many measures of aggregation have been derived but few are useful since most vary with factors other than the aggregation of the animals. Among the most popular indices of aggregation have been the variants of variance (s^2) to mean ($\bar{x}$) ratio (Elliott 1977). Some examples are:

$$\frac{s^2}{\bar{x}},\ \frac{s^2(n-1)}{\bar{x}},\ \frac{s^2}{\bar{x}-1},\ \frac{s}{\bar{x}},\ \frac{100\sqrt{s^2-\bar{x}}}{\bar{x}},\ \frac{(s^2/\bar{x})-1}{\Sigma X-1}$$

where s is the standard deviation, n the number of samples, and ΣX the sum of all animals in a set of replicate samples. The s^2:$\bar{x}$ indices are difficult to apply among sites or dates since apparent aggregation will vary with the mean density even if the variance remains constant. This aspect of the variance to mean ratio might lead to equivalent measures of aggregation if differences in s^2 and $\bar{x}$, between sites or dates, balance each other (Elliott 1977).

Another commonly used index which is also sensitive to variation in $\bar{x}$ is k of the negative binomial distribution ($s^2 = \bar{x} + \bar{x}^2/k$). Morisita's index of contagion (1959; Southwood 1966) is not sensitive to variation in $\bar{x}$ but is susceptible to variation in the area covered by the sampler. It usually cannot be used to compare aggregation between studies.

An index of contagion which can be used to compare aggregation among studies is the exponent in Taylor's Power Law (Taylor 1961). This measure of aggregation incorporates the density dependence of aggregative behavior and is thus free of the confounding effects of density (Taylor et al. 1978). Taylor's Power Function holds well over a range of sampler sizes (Paloheimo and Vukov 1976; Taylor and Taylor 1977), and can be calculated from literature values if some measure of dispersal is given with population data. Another advantage of the power function is that it can describe many types of distributions in one mathematical expression (Taylor 1965; Taylor et al. 1978). The index is calculated as the slope of the relationship between log s^2 and log $\bar{x}$, the exponent b in the expression:

$$(1) \qquad s^2 = a\bar{x}^b$$

where $\bar{x}$ is the arithmetic mean density and s^2 is the variance of a group of replicate samples. The constant a is a sampling factor (Southwood 1966). The exponent b can vary from negative to positive infinity and can describe a variety of distributions (Taylor 1965). Large values of b indicate increasing aggregation; $b > 1$ indicates a contagious distribution. Uniform or equally spaced distributions have $b < 1$. The special case of the random or Poisson distribution ($s^2 = \bar{x}$) occurs when $a = b = 1$.

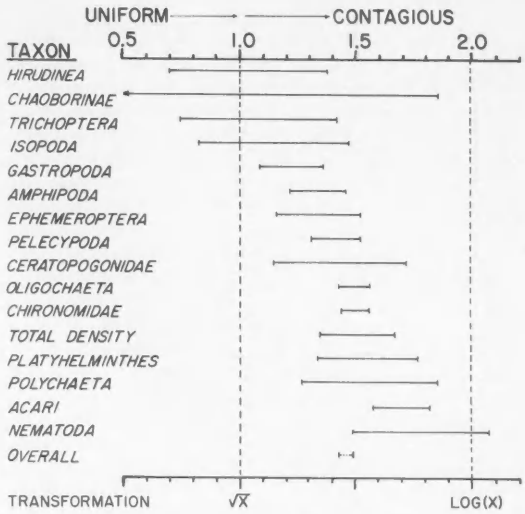

FIG. 1. The degree of contagion in groups of benthic animals shown as 95% confidence intervals of b from equation 1. Values of $b < 1$ indicate that animals are evenly spaced; values of $b > 1$ indicate that animals are aggregated. Transformations shown at the bottom are those values of b under which common transformations would be used (eq. 2).

The measure of aggregation, b, was calculated by simple linear regression analysis for many sets of data. The literature data were sorted and regressed to test the hypothesis that the degree of aggregation is constant among taxonomic groups, among sediment types, and among animals sampled with various sampling gear (Table 2).

Benthic animals in lakes and large rivers are aggregated. All power regressions of variance on the mean show significant positive relationships (Table 2). Most regressions of s^2 on the $\bar{x}$ for group of animals have b significantly greater than 1. Few groups show significantly more or less aggregation than the others (see comparison of b in Fig. 1). Not even the least aggregated animals (lowest b), Hirudineae, Chaoborinae, Trichoptera, or Isopoda are randomly distributed ($a = b = 1$) because even though the confidence intervals of b overlaps one, a is greater than one (Table 2). Further, the variance was less than or equal to the mean in only 2.5% of 1500 sets of data examined. This indicates that the Poisson distribution is not a good model to describe the variability of benthos populations.

The degree of aggregation of animals in various sediment types is very similar as well (Fig. 2). Although all sediments hold animals aggregated to approximately the same extent, there is some tendency for animals to be less clumped in clays and more clumped in gravel (Fig. 2).

The type of sampler used also has little effect on the contagion of the benthos. The Smith-McIntyre grab

TABLE 2. Regression variables for power function regressions of variance (s^2) on mean density (M, m^{-2}) of benthos population estimates where $s^2 = a\bar{x}^b$, n is the number of sets of observations, r^2 is the coefficient of determination, and $1 - b/2$ is the exact variance stabilizing exponent (eq. 2). Chi square tests (Tsutakawa and Hewett 1977) were used to determine whether the regression lines are significantly different from the overall regression of log s^2 on log $\bar{x}$. Significant values of χ^2 indicate that the regression line shows a higher (+) or lower (−) variance overall. Asterisks indicate that test statistics are significant at $P < 0.01$ (**) or $P < 0.05$ (*), ns = not significant.

Data set	n	r^2	a	b	$1-b/2$	χ^2 test
Groups of animals						
Acari	22	0.98**	3.03	1.708	0.15	ns
Amphipoda	92	0.84**	10.45	1.339	0.33	ns
Ceratopogonidae	5	0.99**	6.47	1.434	0.28	ns
Chaoborinae	4	0.94**	31.19	1.043	0.48	ns
Chironomidae	387	0.85**	3.94	1.498	0.25	ns
Ephremeroptera	47	0.83**	7.57	1.339	0.33	ns
Gastropoda	128	0.71**	11.48	1.223	0.39	ns
Hirudinae	34	0.54**	18.58	1.041	0.48	ns
Isopoda	10	0.89**	20.46	1.149	0.43	ns
Nematoda	24	0.88**	0.61	1.781	0.11	ns
Oligochaeta	286	0.86**	4.92	1.496	0.25	ns
Pelecypoda	138	0.83**	7.87	1.496	0.29	*(+)
Platyhelminthes	34	0.87**	4.18	1.557	0.22	ns
Polychaeta	13	0.92**	3.24	1.561	0.22	ns
Trichoptera	29	0.63**	13.21	1.084	0.46	ns
Total number	154	0.69**	3.10	1.512	0.24	**(−)
Type of sediment						
Clay, mud, gravel	29	0.78**	8.30	1.223	0.39	ns
Mud and detritus	31	0.84**	5.35	1.253	0.37	**(−)
Clay and sand	81	0.82**	8.22	1.259	0.37	ns
Clay and silt	58	0.63**	17.18	1.336	0.33	ns
Sand and mud	175	0.79**	7.59	1.340	0.33	ns
Sand and silt	106	0.75**	9.75	1.358	0.32	ns
Sand	95	0.85**	6.81	1.369	0.32	ns
Silt	121	0.88**	6.04	1.840	0.31	ns
Fluid mud	8	0.60*	24.21	1.411	0.29	ns
Sagittaria	12	0.74**	8.73	1.418	0.29	ns
Mud and gravel	30	0.70**	5.09	1.423	0.29	ns
Sand and gravel	71	0.87**	6.27	1.461	0.27	ns
Gravel	110	0.84**	5.04	1.468	0.27	ns
Mud	466	0.89**	5.16	1.495	0.25	ns
Fine sand	34	0.85**	1.68	1.687	0.16	ns
Type of sampler						
Allen Sampler	10	0.97**	16.00	1.323	0.34	*(+)
Ekman Grab	301	0.79**	18.97	1.247	0.38	ns
K-B Corer	37	0.87**	6.82	1.574	0.21	**(+)
Marukawa	10	0.74**	115.08	1.404	0.30	**(+)
Multiple Corer	4	0.99**	16.48	1.368	0.32	ns
Modified Ekman	7	0.97**	4.44	1.595	0.20	ns
Maitland Corer	4	0.99**	17.54	1.527	0.24	ns
Pearson Airlift	34	0.94**	12.25	1.467	0.27	**(+)
Petersen Grab	722	0.82**	6.43	1.343	0.33	ns
Ponar Grab	266	0.81**	7.31	1.399	0.30	*(−)
Smith-McIntyre	20	0.89**	1.29	1.764	0.12	ns
Surber	18	0.93**	5.00	1.531	0.23	ns
Overall	1462	0.87**	5.24	1.462	0.27	

gives rise to the highest b (most aggregation), possibly due to the intermittent loss of some surface sediments from pressure wave effects (Fig. 3).

In all cases differences in exponents are small. The greatest variation in b is seen when data are regressed within taxa (Fig. 1–3). Tests of the hypothesis that groups of data vary from the overall regression of log s^2: log $\bar{x}$ show that few sets of data lie significantly above

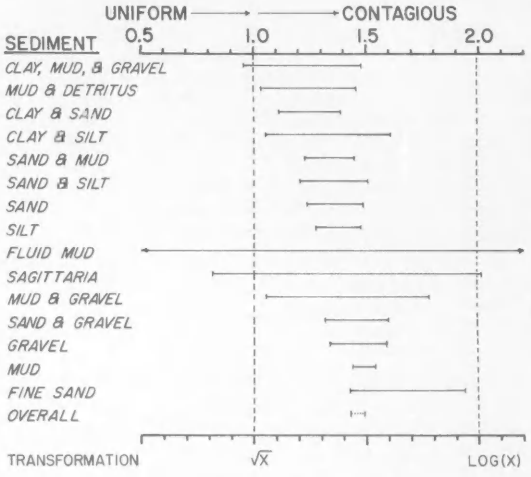

FIG. 2. The degree of contagion of benthic animals in various substrates shown as the 95% confidence intervals of b from equation 1. Values of $b < 1$ indicate that animals are evenly spaced; values of $b > 1$ indicate that animals are aggregated. Values of b under which common transformations would be used are shown at the bottom of the figure (eq. 2).

or below the overall s^2:$\bar{x}$ regression (Table 2) (nonparametric technique of Tsutakawa and Hewett 1977). The tests show that pelecypods yield a variance which is higher than expected for any given density and that counts of total benthos populations and populations collected from mixtures of mud and detritus yield a variance which is lower than expected for any density. When regression lines are calculated on data grouped by sampler there are significant differences among these regressions in spite of fairly uniform slopes (Fig. 3). These differences among regressions are probably due to elevation (increased a) which indicates that a is indeed a factor related to sampling conditions (Southwood 1966). The amount of aggregation (b), though, is roughly the same over all types of animals, sediments, and samplers.

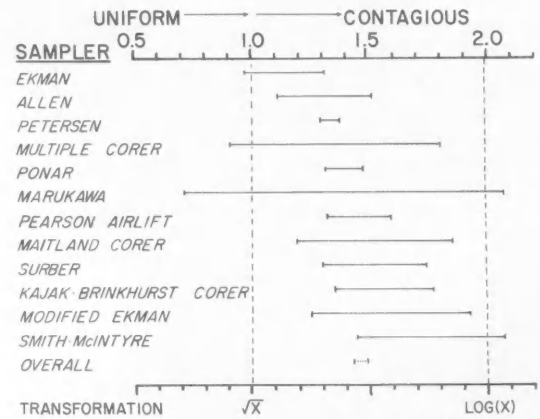

FIG. 3. The degree of contagion of benthic animals taken with various sampling gear shown as the 95% confidence intervals of b from equation 1. Values of $b < 1$ indicate that animals are evenly spaced; values of $b > 1$ indicate that animals are aggregated. Values of b under which common transformations would be used are shown at the bottom of the figure (eq. 2).

The similarity of aggregation among groups of pooled data is not the result of broad confidence intervals due to failure to account for differences in aggregation (b) among sampling sites or investigators. If different systems or investigators gave rise to data aggregated in different ways, then pooled data would be made up of many different s^2:$\bar{x}$ relationships. A test of the homogeneity of data within a pooled regression should give us more confidence that we are not merely generating broad regressions which cannot be separated due to their heterogeneity. Mori (1976) studied the benthos of Lake Biwa (Japan) during 1972 and presented tables of raw data. Log–log regressions of variance and mean for homogeneous data (oligochaetes within sampling stations) were not different from the overall regression of log s^2 on log $\bar{x}$ (chi square tests, $P \geq 0.01$). The similarity of the most homogeneous data with the over-all regression was an example chosen at random which indicates the homogeneity of s^2:$\bar{x}$ data. Log–log regressions of s^2 on $\bar{x}$ for oligochaetes within stations had r^2 values: 0.01 at station Ie-1; 0.39 at station Nb-2; 0.03 at station Nb-5; and 0.60 at station Na-3. These r^2 values are all lower than the r^2 of 0.86 from pooled oligochaete data (range of $\bar{x}$ within stations approximately equal to that overall). This example indicates that the maximum probability of separating slopes of log s^2:log $\bar{x}$ relationships (b), and thus separating differences in contagion, would be found in pooled calculations. The similarity of contagion among taxa, sediments, and samplers is real and reflects the basic similarity of the distribution of most types of benthos.

TRANSFORMATION

In order that parametric statistical methods may be applied to benthic data, the assumptions of normal analysis of variance must be satisfied. Some of the major assumptions of the analysis of variance are that the data are normally distributed, the errors are equal and uncorrelated with the magnitude of the means, and that the variance components are additive (see Scheefé 1959 for a thorough review). The seriousness of violating these assumptions will vary with the sort of hypothesis to be tested and the nature of the data. Scheefé (1959) found that if the number of samples is very large and constant among treatments, and both the skewness and kurtosis are constant among samples, then differences among means may be tested safely using parametric techniques without transformation to stabilize the vari-

ance. These conditions are rarely met in benthos studies since the number of samples obtainable at each station is often limited and the shapes of benthos density distributions vary widely. The consequences of this sort of violation of the assumptions of the analysis of variance can be severe and can cause invalid statistical inference (Scheefé 1959).

In many cases transformation will cause data to meet the assumptions of parametric analysis adequately. Many authors feel that transformation to stabilize the variance (remove correlation between the variance and the mean) will help to alleviate skewness in the distribution and increase the probability of additivity (Bliss and Owen 1958; Snedecor and Cochran 1967; Southwood 1966; Tukey 1968). Many types of analysis can be made more valid through transformation to stabilize the variance. These include: those analyses emyploying *F*- or *t*-tests (Aveson and Schmitz 1970; Snedecor and Cochran 1967), linear regression (Hocking 1976), and the randomized complete block design (Lindsey 1976). In some cases, transformation to stabilize the variance will not be adequate and the conformity of the data to the assumptions of the analysis of variance should be tested (Scheefé 1959).

Taylor (1961) showed that an exact variance stabilizing function (transformation) can be calculated if the power relationship of the variance to the mean (eq. 1) is known. This paper (Table 2; Fig. 1, 2, 3) and many others (see Southwood 1966 for review) demonstrate that in ecological data the variance often increases with the mean ($b > 0$). Taylor (1961) found that this relationship obeys a power law and that the variance in groups of population estimates can be stabilized by transforming the original data:

$$X' = X^{1-b/2} \tag{2}$$

where X is an individual population estimate (number of animals in single grab sample or number m^{-2}), X' the transformed datum, and b is the exponent found in equation 1. If b is 1 then the square root transformation is used, if b is 2 then the log transformation has been recommended (Taylor 1965). For all other situations exact transformations can be calculated. Normal statistical methods are performed using the transformed data.

Because the slope of the log–log regressions of variance and mean of benthic population estimates are all approximately the same (Fig. 1–3), a transformation suitable for all benthic data can be derived. Exact transformations for specific types of data are listed in Table 2. Few exact power transformations are significantly different from the others regardless of type of animal, sediment, or sampling gear used. Exact transformations for benthic data seldom overlap the square-root transformation ($b = 1$, $1 - b/2 = 0.5$) or the log transformation ($b = 2$, $1 - b/2 = 0$) which are the common transformations recommended for the transformation of benthic population estimates (Elliott 1977). A universal transformation calculated from the overall regression of s^2 and $\bar{x}$ (Table 2), is not significantly different from the fourth-root transformation. That is:

$$X' = X^{0.25} \tag{3}$$

This transformation can be applied successfully to most benthic data.

The utility of the fourth root transformation in the analysis of benthic data is illustrated in Table 3. If the transformation is adequate then transformed data should show no relationship between the variance and the mean. Table 3 shows r^2 values for log–log regressions between the variance and the mean of untransformed and transformed data. All untransformed data show significant relationships between variance and mean; loss of the significant relationship after transformation indicates that the variance was stabilized by the transformation. The fourth-root transform always stabilized the variance while the square-root and log transformations recommended by Elliott (1977) failed in some cases. In cases where the r^2 after fourth-root transformation is large but not statistically significant, more stability could be gained by attention to the exact size

TABLE 3. Coefficients of determination (r^2) of relationship between $\log_{10}s^2$ and $\log_{10}\bar{x}$ for untransformed data and data transformed with the square root ($x^{0.5}$), fourth root ($x^{0.25}$), and logarithmic ($\ln [x+1]$) transformations. * indicates that there is a significant ($P < 0.05$) correlation between s^2 and $\bar{x}$. Only samples with greater than three organisms per sampler were included because s^2 cannot be stabilized if $\bar{x} \leq 3$ (Andersen 1965).

Author/Station	n	r^2				b
		Untransformed	$x^{0.5}$	$x^{0.25}$	$\ln (x+1)$	
Hiltunen (1971)/#1	14	0.68*	0.05	0.18	0.26	1.34
Hiltunen (1971)/#1	7	0.76*	0.07	0.23	0.72*	1.18
Hiltunen (1971)/#4	12	0.67*	0.05	0.17	0.07	1.60
Koss et al. (1974)/1G	7	0.73*	0.34	0.09	0.01	2.28
Mori (1976)/Nb-2	10	0.72*	0.17	0.007	0.01	1.80
Mori (1976)/Na-3 (Jan.–Dec.)	18	0.61*	0.22*	0.04	0.001	2.04
Mori (1976)/Na-3	6	0.97*	0.86*	0.60	0.34	2.36

TABLE 4. Analysis of variance table for regression of $\log_{10}s$ predicted by $\log_{10}M$ ($\bar{x}\cdot m^{-2}$) and area covered by sampler (eq. 4). F' (partial F value) is calculated as the increase in Model SS when the variable in question is entered into the multiple regression as the last variable. F' is a measure of the variation in $\log_{10}s$ accounted for by each independent variable. The probability of gaining any of these F and F' values by chance is $\ll 0.0001$.

Source of variation	df	SS	F	r^2
Model ($\log_{10}s = \log_{10}M$ + Area)	2	718	5285	0.88
Error	1433	97		
Total	1435	816		
Independent variable	F'			
$\log_{10}M$	7456			
Area	84			

of b in equation 2, rather than using the universal approximation of $b = 1.5$ ($1 - b/2 = 0.25$). If b, calculated for the specific set of data, is significantly different from 1.5, the exact transformation should be used and not the universal one (eq. 3). This will lead to more frequent satisfaction of the assumptions of parametric analysis.

Design of Sampling Programs

The primary concern in designing a sampling scheme is to gain an accurate measurement with high precision for the least effort. The size of the sampler or quadrat, and the number of replicate samples taken can be varied so that the minimum number of samples of minimum size may be extracted to yield a specified degree of precision. To date, the only means of calculating the number of samples needed to yield a certain precision has been to make some assumptions about the distribution of data and the relationship of the variance to the mean (Elliott 1977). Knowing the relationship of sample variance to density, sampler size, and number of samples taken would permit precise estimation of sampling requirements (Cochran 1977).

I have shown that the variance of a set of replicates is predictable from the mean density alone with a high degree of precision (Table 2). Using multiple regression analysis, I have found that the standard deviation(s) is predictable from the mean density, and that a significant amount of residual variation in the standard deviation is accounted for by sampler size (Table 4). The regression equation ($r^2 = 0.88$) to predict the standard deviation (s) is:

$$(4) \quad \log_{10}s = 0.581 + 0.696 \log_{10}M - 2.82 \times 10^{-4}A$$

where M is the mean density in numbers m^{-2} and A is the area of the sampler in cm^2. The equation will provide unbiased predictions of $\log_{10}s$ in spite of the fact that M is measured with error, provided that M is measured under the same experimental conditions as those that were used to produce the regression equation (Guest 1961). This regression holds within the range of M of 3.0–48 000, the range of A of 15.2–2500, and the number of replicates from 2 to 54.

The precision of predictions made with equation 4 is shown as a comparison of observed and predicted values in Table 5. The observations in Table 5 were not used in the sampling survey from which the regression was derived, nor were any data from that lake or data collected with that sampler included. Observed and predicted standard deviations are quite similar. Predictions deviate from observations by 5 to 50% of the observed standard deviation.

Equation 4 can be used to predict s for proposed sampling surveys. The input variables are only the size of available sampling gear and the mean density of animals to be encountered. A guide to the distribution of densities of taxa and groups of taxa (Fig. 4) can be used to guess at the densities which will be encountered in the field.

Because the standard error (SE) is $s/\sqrt{n}$, and $SE/\bar{x}$

TABLE 5. Comparison of observed and predicted standard deviation(s) for data from Krezoski et al. (1978). Predicted values of s are from equation 4. Columns labelled $\hat{s}$ are values of s predicted using the Poisson or negative binomial models (Elliott 1977).

Sample: Sample	Number m^{-2}	Observed s	Predicted s (this paper)	$\hat{s}$:Poisson	$\hat{s}$:$k=2$
Station 14					
Amphipoda	2912	1015	959	54	2059
Diptera	48	111	55	7	35
Oligochaeta	5661	2099	1524	75	4003
Pelecypoda	471	371	270	22	334
Total number	9092	2470	2120	95	6429
Station 18					
Amphipoda	2678	838	904	52	1894
Mysidacea	48	111	55	7	35
Oligochaeta	634	617	333	25	449
Pelecypoda	705	530	356	27	499
Total number	4065	1053	1209	64	2875

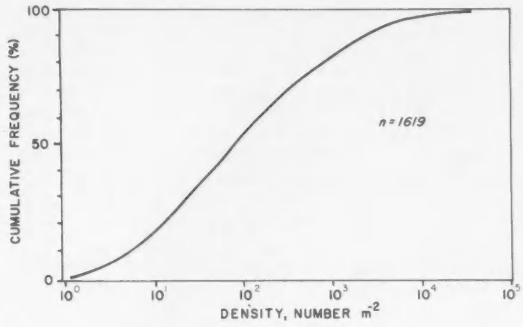

FIG. 4. Cumulative percent frequency of macrobenthos found in literature survey. This figure should be read "Y% of benthos densities are less than X m^{-2}."

is a good measure of precision, we can use equation 4 to optimize sampling programs. The most probable SE can be calculated:

$$(5)\quad \text{SE} = (\text{antilog}\,(0.581 + 0.696 \log M - 2.82 \times 10^{-4} A))/\sqrt{n}$$

where n is the number of replicate samples. Rearranging equation 5 slightly and substituting the acceptable level of precision (P) in terms of M in place of the SE:

$$(6)\quad n = (\text{antilog}\,(0.581 + 0.696 \log M - 2.82 \times 10^{-4} A))/PM^2$$

For example, if the desired level of precision is SE equal to 20% of the mean density, then $P = 0.2$. Solving equation 6 will tell us the most probable number of samples of any size we must take to gain the precision P at any density of animals. It should be noted that the confidence region around a predicted s will not be symmetrical due to the log transform in equation 4.

Because equations are difficult to evaluate, some example calculations of the number of samples necessary to obtain a precision of $\text{SE}/\bar{x} = 0.2$ for various sampler sizes and densities are provided in Table 6. These calculations show that more samples must be taken with small samplers and more samples must be taken at low density in order to obtain the same level of precision.

The objective in optimizing sampling programs is to gain the best precision for the least effort. In most benthic studies much of the effort is expended in processing the sediment (e.g. sieving, washing, counting). Optimization usually requires processing the least sediment for the greatest precision. The amount of sediment processed for a SE of 20% of the density can be found by multiplying the figures in Table 6 by the area of the sampler. The smaller numbers in Table 7 show which regime is the most profitable. Where processing sediment makes up the greatest portion of the sampling labor, the amount of work necessary to gain any level of precision decreases as the density of the population under study increases. The amount of work necessary increases with the size of the sampling device. Where sampling itself is difficult, subsampling of large samples might be considered. Statistical inference would only be valid to the large sample, if subsampling is used.

Looking back to Fig. 4 and Table 6 it is obvious why many benthic population estimates seem variable. In studies with replicate estimates the most frequent number of samples taken was 3. In such studies a SE equal to 20% of the mean density would be found consistently only at density greater than 1000 animals m^{-2}. Less than 20% of the densities of benthos found in nature lie above 1000 animals m^{-2} (Fig. 4) and thus 80% of the SE's found taking three replicates will be greater than 20% of the mean. This situation could easily be remedied by taking many samples with a small sampler, thus increasing precision without much increase in effort (Table 7).

The technique presented here for planning sampling surveys differs from that of Elliott (1977) in that no assumptions are made regarding the distribution of benthic animals in nature. Elliott's technique requires the adoption of an algorithm for calculating the variance (s^2), then dividing s by $\sqrt{n}$ to calculate the expected SE. The formula for s^2 depends upon the assumed distribution which is either measured once or simply guessed and assumed to remain constant. Elliott (1977) sug-

TABLE 6. Number of replicate samples needed for various sampler sizes and macrobenthos densities in order that the SE of replicate samples average 20% of the mean density. Calculations are from eq. 6.

Density	Size of sampler (cm^2)						
number m^{-2}	20	50	100	250	500	750	1000
30	32	31	30	24	17	13	9
50	24	23	21	18	13	9	7
100	16	15	14	12	8	6	4
300	8	8	7	6	4	3	2
500	6	6	5	4	3	2	2
1000	4	4	3	3	2	<2	<2
5000	<2	<2	<2	<2	<2	<2	<2
10 000	<2	<2	<2	<2	<2	<2	<2

TABLE 7. Area of sediment (cm^2) that must be sampled, sieved, and sorted in order that the SE of replicate samples average 20% of the mean density, for various sampler sizes and macrobenthos densities. Figures are number of samples (Table 5) multiplied by the area of the sampler used. Calculations are from Table 5.

Density	Size of sampler (cm^2)						
number m^{-2}	20	50	100	250	500	750	1000
30	640	1550	3000	6000	8500	9750	9000
50	480	1150	2100	4500	6500	6750	7000
100	320	750	1400	3000	4000	4500	4000
300	160	400	700	1500	2000	2250	2000
500	120	300	500	1000	1500	1500	2000
1000	80	200	300	750	1000	1500	2000
5000	40	100	200	500	1000	1500	2000
10 000	40	100	200	500	1000	1500	2000

gests that the Poisson distribution where $s^2 = \bar{x}$ or the negative binomial distribution ($k = 2$) where $s^2 = \bar{x} + (\bar{x}^2)/k$ provide good approximations of the variability of benthos samples. The equation which I present for calculating s (eq. 4) is empirically derived from published data. The advantages of the empirical technique can be seen when compared to the results assuming the Poisson or negative binomial with constant k (Table 5). If the Poisson is assumed when planning a sampling survey, then s will be underestimated and too few samples will be taken. If the negative binomial is assumed, then in some cases s will be greatly overestimated and too many samples will be taken.

The findings of this study will hold provided that future experimental techniques are similar to those which were included in the data set used here. For example, care should be taken to use a sampling technique suited to the substrate (Kajak 1971) so that no extra variability is introduced through improper sampling. All substrates are not represented in all sampler classes (Table 2) so this is an important consideration.

Though the data set is adequate for this analysis, I am constantly adding data for the testing of further hypotheses. Any quantitative data that readers have available would be welcomed.

SAMPLING THE STREAM BENTHOS

Recently a paper was published by Resh (1979) in which the stream benthos data of Needham and Usinger (1956) and Chutter and Noble (1966) were examined to find the number of samples required to gain a specified precision at various benthos densities. Resh found that the number of samples necessary to gain a specified precision increased with decreasing density. This result is similar to that shown in my Table 6 so I have compared one set of these streams benthos data with eq. 4 which was derived from the benthos of lakes and large rivers (Fig. 5). The predictions from eq. 4 are significantly lower than the variability seen by Chutter and Noble (1966) (Fig. 5) as well as the variability seen by Needham and Usinger (1956). This suggests that the benthic animals of stream riffles are more variable than those of lakes and rivers, and that sampling programs for stream benthos should be constructed accordingly.

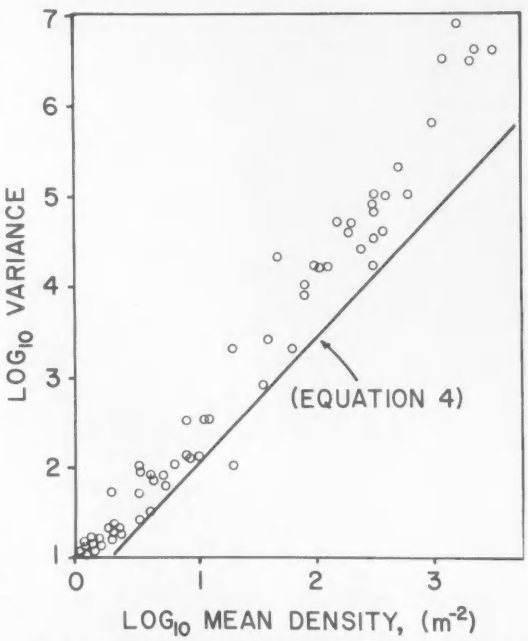

FIG. 5. The relationship of the variance to the mean in stream benthos samples compared to the relationship predicted by eq. 4. The stream benthos data are taken from Chutter and Noble (1966); each data point represents the mean and variance of a taxon (10 samples each). The least-squares regression equation to describe s^2 is: $s^2 = 7.24\bar{x}^{1.61}$ ($n = 69$; $r^2 = 0.97$). The figure shows that the benthos of lakes and large rivers are somewhat less variable than the benthos of a stream riffle.

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Detection of Bacterial Kidney Disease in Wild Salmonids in the Margaree River System and Adjacent Waters Using an Indirect Fluorescent Antibody Technique

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The indirect fluorescent antibody technique demonstrated the enzootic nature of bacterial kidney disease in 224 of the 605 wild salmonids sampled from the Margaree River system and some adjacent waters. Asymptomatic infections were observed in 33.4% of 456 Atlantic salmon (*Salmo salar*) parr and 35.1% of 37 returning adults in samples taken from the source of the Margaree River to and including saltwater areas off the coast.

Key words: kidney disease, Atlantic salmon, wild, distribution, fluorescent antibody

PATERSON, W. D., C. GALLANT, D. DESAUTELS, AND L. MARSHALL. 1979. Detection of bacterial kidney disease in wild salmonids in the Margaree River system and adjacent waters using an indirect fluorescent antibody technique. J. Fish. Res. Board Can. 36: 1464–1468.

La nature enzootique de la maladie bactérienne du rein fut démontrée, au moyen de la technique anticorps par fluorescence indirecte, chez 224 des 605 salmonidés sauvages échantillonnés dans le réseau de la rivière Margaree et eaux avoisinantes. Des infections asymptomatiques ont été observées chez 33,4% des 456 tacons de saumon atlantique et 35,1% des adultes revenant en eau douce, dans des échantillons prélevés depuis la source de la rivière Margaree jusqu'aux régions d'eau salée du large de la côte inclusivement.

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SINCE bacterial kidney disease (KD) was first described in North America (Belding and Merrill 1935), its presence has been identified in numerous hatchery stocks in United States and Canada (Earp et al. 1953; Rucker et al. 1954; Bell 1961; Warren 1963; Pippy 1969; Frantsi et al. 1975; Yamamoto 1975). The severity of this disease in hatcheries varies from a low but detectable infection causing no overt problems to a chronic annually occurring disease causing heavy mortalities (Warren 1963). The Canadian Government Fish Culture Station on the Margaree River in Cape Breton, Nova Scotia is a hatchery in which Atlantic salmon (*Salmo salar*) suffer heavy annual KD caused losses during smolting stage (Frantsi et al. 1975; Pippy 1969).

Although data accumulate regarding the presence of this disease in cultured salmonids, few reports exist about the presence and distribution of KD in wild fish (Wood and Wallis 1955; Evelyn et al. 1973; MacLean and Yoder 1970; Pippy 1969; Frantsi et al. 1975; and Ellis et al. 1978). Recently, the introduction of the more sensitive indirect fluorescent antibody technique (IFAT) (Bullock and Stuckey 1975) has allowed detection of asymptomatic or covert (no lesions) as well as symptomatic or overt (lesions) KD infections.

In this report, IFAT was used to monitor wild salmonids of the Margaree River, its tributaries and some adjacent rivers for the presence of KD to describe more accurately distribution of KD in the area.

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Materials and Methods

Sampling — Wild Atlantic salmon parr and brook trout (*Salvelinus fontinalis*) were electroseined in the summer of 1977 from various waterways in the Margaree area of Cape Breton. Although an experimental design aim of 10 trout and 10 salmon per sampling station was set, the numbers of fish available often dictated the actual sample size. Samples of returning adult Atlantic salmon trapped commercially off the Cape Breton Island (Nova Scotia) coast and angled in the Margaree sport fishery were monitored for KD. We also examined formalin-preserved Atlantic salmon parr electroseined from various Margaree Valley waters by Dr P. Elson in 1957 and 1965–68. Kidney smears from each fish were made on acetone-cleaned glass slides which were

TABLE 1. Comparison of methods used to diagnose bacterial kidney disease.[a]

	Presence of lesions	Presence of Gram-positive rods in kidney smears	Presence of small nonmotile rods in kidney (Phase of moist mount)	Presence of fluorescing bacteria (Using IFAT)	Culture of BKD organism
Positive for BKD	22/50	17/47	22/50	47/50	29/50
% Incidence of BKD	44	36	44	94	58

[a]A heavily infected population of live 2-yr-old smolting Atlantic salmon was used.

then stained according to the IFAT of Bullock and Stuckey (1975).

Detection methods — During preliminary work to assess various KD detection techniques, the following diagnostic procedures were compared:

1) Presence of symptomatic or overt KD infections as expressed by exterior blebs or gross lesions on internal organs (kidney, spleen, liver, stomach, intestine, heart) containing small Gram-positive rods (Belding and Merrill 1935; Earp et al. 1953; Smith 1964).
2) Presence of small Gram-positive rods in kidney smears in presence or absence of overt infections (Belding and Merrill 1935).
3) Presence of small, nonmotile diplo-bacilli in moist mounts of kidney tissue viewed by phase contrast microscopy.
4) Growth of the KD causative agent at 15°C when kidney material was streaked undiluted on Mueller Hinton agar containing 0.1% L cysteine hydrochloride and 10.0% fetal calf serum.
5) Presence in kidney smears of fluorescing bacteria of typical size and shape using IFAT (Bullock and Stuckey 1975).

A particular KD-infected population of 2-yr-old smolting hatchery Atlantic salmon was monitored by all of the above procedures and the detection frequency of each method was compared.

The relative sensitivities of detection using the IFAT technique and the immunodiffusion test (Chen et al. 1974) were also determined separately. Suspensions of BKD organisms, enumerated using a Petroff-Hausser bacterial counting chamber, were added to a known weight of macerated fish kidney prior to the above examination.

Microscopy — Kidney smears were examined on a Zeiss photomicroscope using a 63× plano apochromatic phase objective and bright field (for Gram stain), phase contrast microscopy (for moist mount) and UV epifluorescence (for IFAT).

Results

The use of IFAT revealed an incidence of KD about twice that demonstrated by the other techniques (Table 1). Isolation and culture of the causative agent on the supplemented Mueller Hinton Medium proved to be less sensitive than IFAT, but more sensitive than the generally practiced diagnosis by Gram stain. Using IFAT to observe fish kidney tissue to which KD cells had been added, an infection density of 1.4×10^7 KD cells/g of kidney was readily detectable providing several fluorescing bacteria per field. The immunodiffusion technique required a cell density of 1.4×10^9 KD cells/mL saline for detection but the technique failed to detect the bacteria at this level when they were mixed with kidney tissue.

The examination of formalin-preserved samples showed that KD has been present in Cape Breton Island for at least 20 yr (Fig. 1, Table 2). Every tributary of the Margaree system except for the Calumruadh Brook proper, contained KD-infected trout and/or salmon. In addition, KD was detected in many adjacent rivers including the Cheticamp River, Mabou River, Judique Interval Brook, Baddeck River system, and the Middle River system, all locations where there had been no previous history of KD.

Although none of the fish examined had overt or symptomatic KD infections, the kidneys of two salmon parr caught near the source of the Margaree R. (on the North Branch of the Northeast Margaree R.) were shown by IFAT to be heavily infected with KD bacteria (200 bacteria per 788× microscope field). This suggests that chronic advanced infections, severe enough to cause death, may occur in nature.

The presence of KD was also observed in the kidney smears taken from returning adult Atlantic salmon caught in commercial saltwater traps.

Discussion

The IFAT described by Bullock and Stuckey (1975) has facilitated detection and serological confirmation of both overt and covert KD infections, many of which would have been missed by other procedures. An improved culture technique, recently described by Evelyn (1977), was, however, not tested. Previously KD has been demonstrated in only a few wild Margaree salmon, all of which had overt infections (Pippy 1969; Frantsi et al. 1975). In these reports the presence of overt infections led to diagnosis of KD using gram stains of internal organ smears. If covert infections had been diagnosed as well, the incidence would probably have been considerably higher.

How much reliance should be placed on this IFAT test which yields a much higher incidence of KD infections? Although the IFAT does not provide viable cultures which can be utilized to reinfect fish and satisfy Koch's postulates, it does clearly detect and serologically con-

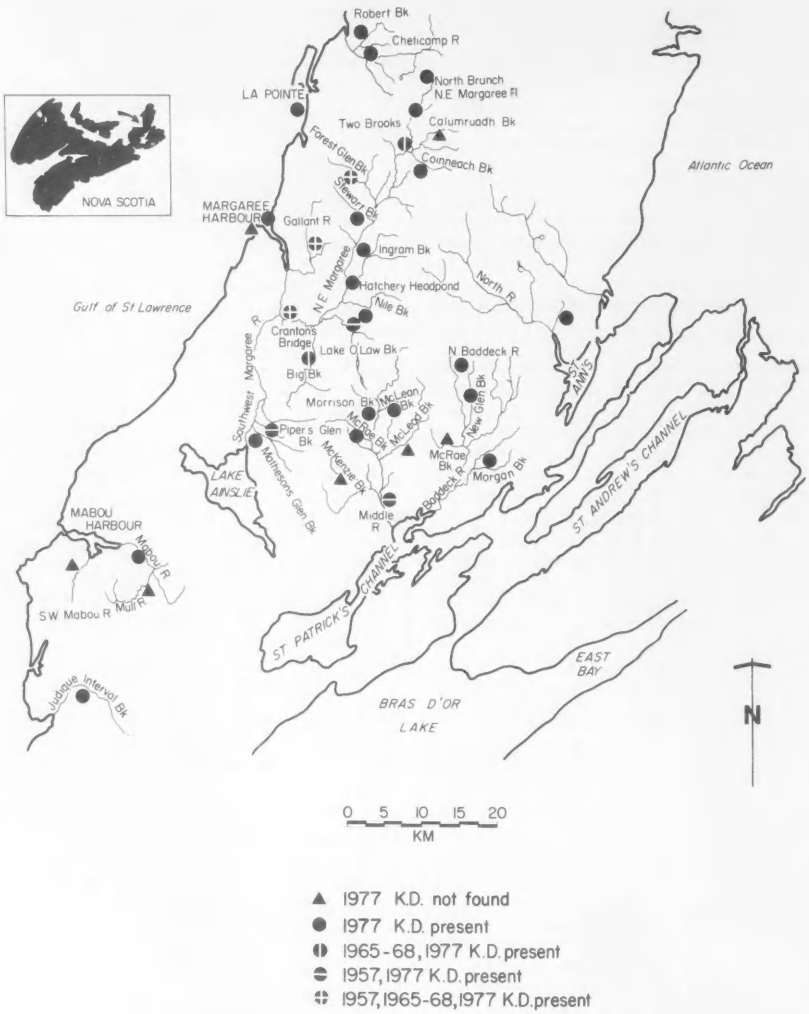

FIG. 1. Incidence of bacterial kidney disease in wild salmonids in the Margaree River, tributaries of the Margaree and some adjacent Cape Breton rivers using an indirect fluorescent antibody technique.

firm the presence of this antigenically homogeneous and uniquely sized bacterium when present in significant numbers within the kidney (1.4×10^7 KD bacteria/g kidney). For survey work IFAT satisfied a timely need. However, attention should be paid, not only to the qualitative presence, but also to the quantitative density of bacteria in the kidney.

The data in this report indicate that a pool of KD infection exists in nature at a high level among salmonids of various ages and raises the question of transmission routes and virulence in the wild. The demonstration of kidney disease in wild Margaree system Atlantic salmon parr sampled in 1957, 1965–68, and 1977, indicates the enzootic nature of this disease in the watershed during at least the last 20 yr. There have been other reports of KD infections in wild immature salmon (Rucker et al. 1953; Pippy 1969; and Frantsi et al. 1975) but the widespread nature of covert infection among wild salmonid stocks was not observed.

Bacterial kidney disease infections have also been observed among returning adult Pacific and Atlantic salmon (Wood and Wallis 1955; MacLean and Yoder

TABLE 2. Incidence of bacterial kidney disease in wild Atlantic salmon[a] and eastern brook trout found in the Margaree River, its tributaries and in some adjacent rivers during the period 1957 to 1977.

Location	1957	1965–68	1977	
	Salmon percent incidence (*n*)	Salmon percent incidence (*n*)	Trout percent incidence (*n*)	Salmon percent incidence (*n*)
Northeast Margaree R. Headwaters				
Northeast Margaree R.		45 (20)	100 (6)	63 (27)
(Calumruadh Bk. to Mouth)	30 (20)	33 (15)	50 (4)	31 (93)
				adults 37.5 (24)
Calumruadh Bk.				0 (6)
Coinneach Bk.				50 (4)
Forest Glen Bk.	18.7 (16)	30 (20)	14 (7)	61.5 (13)
Stewart Bk.			10 (10)	50 (10)
Ingram Bk.			29 (17)	30 (18)
Nile Bk.			14.3 (14)	85.7 (7)
Lake O'Law Bk.	40 (14)		11.1 (9)	20 (10)
Big Bk.			10 (10)	0 (10)
Gallant River	31.2 (16)	26.6 (15)	40 (10)	30 (10)
Southwest Margaree R.				
Pipers Glen	25 (4)		70 (10)	
Matheson Glen				53 (17)
Adjacent Rivers				
Cheticamp River			29 (7)	9 (11)
Robert Bk.			100 (1)	50 (2)
Judique Intervale Bk.				70 (10)
Mabou River				28.6 (7)
Mull River				0 (5)
Middle River and tributaries	15 (20)		43 (7)	0 (10)
				adults 0 (2)
Baddeck River and tributaries				58 (26)
				adults 0 (2)
Gulf of St. Lawrence — saltwater				
Margaree Harbour				adult 100 (1)
Whale Cove				adult 0 (2)
La Pointe				adult 33 (6)

[a]Salmon parr unless otherwise specified.

1970). In the present work using IFAT diagnosis, 37.5% of examined adult Atlantic salmon reurning up the Margaree River were covertly infected with KD and 33% of a group of adults trapped in saltwater at La Pointe also had covert KD infections. Detection of KD in salmon taken commercially in saltwater traps near La Pointe suggests that these animals had contracted KD infection sometime during their life cycle prior to ascent of freshwater streams. In experimental seawater, cage culture of selected Pacific salmon, the progression of KD in salt water led ultimately to significant losses and constituted the major cause of death in sockeye and chinook salmon as these animals approached market size. (T. P. T. Evelyn, Department of Fisheries and Oceans, Nanaimo, B.C. personal communication; Kennedy et al. 1976, 1977). Overt KD infections also occur in wild salmon in salt water. Ellis et al. (1978), reported the isolation of the causative agent of KD from lesions on the kidney and heart of an immature chinook salmon found in seawater; the first record of a KD infected fish found at sea.

Many questions about the effect of KD on Atlantic salmon populations exist, although parr density studies of the last 20 yr have contributed some data in this regard. The incidence of KD in Atlantic salmon of Forest Glen Brook was 18.7% in 1957 through 50% between 1965 and 1968 to the current 61.5% in 1977. The densities of Atlantic salmon parr taken at three sites on Forest Glen Brook were 51.2 ± 22.4 (SD)/100 m^2 between 1957 and 1961, 88.9 ± 30.6 (SD)/100 m^2 in 1966–68 and 35.5 ± 12.1 (SD)/100 m^2 in 1975–77. The high densities in 1966–68 were attributed to benefits from temporary predator (fish-eating ducks) control program. Although current parr densities are lower than expected from recent high densities of salmon fry, they are in fact not significantly lower than a density of 38.3 parr/100 m^2 which Elson (1967) determined to be a "normal" abundance for

unsprayed rivers of New Brunswick. These data suggest that wild salmon parr can exist at a "normal" density in the presence of KD.

The presence of steady populations of Atlantic salmon parr over a 20-yr period during which KD had been enzootic in the area, indicates that these fish survive in the presence of the disease. A similar investigation for other stages of salmon such as smolt and adult is needed before we can accurately evaluate the effect of KD on wild fish populations and the significance of covert infections.

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Polycyclic Aromatic Hydrocarbon Carcinogens in Commercial Seafoods

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Fresh and processed commercial seafoods were analyzed for the polycyclic aromatic hydrocarbon carcinogen benzo(*a*)pyrene using a thin-layer chromatographic separation technique and quantitation by fluorescence. Commercial samples of vertebrate fish did not contain detectable levels, except where fish were packed with vegetable oil, an exogenous source of carcinogens. Levels in most shellfish samples were generally less than 10 ng/g wet weight, but occasional samples contained up to 36 ng/g. Crab and shrimp samples contained little or no benzo(*a*)pyrene (ND to 0.5 ng/g). Commercial lobsters contained 0.8 to 7.9 ng/g. The source of contamination of lobsters was further investigated, utilizing high pressure liquid chromatography to measure 13 polycyclic aromatic hydrocarbon isomers. Freshly caught lobsters had less than 1 ng/g benzo(*a*)pyrene. Lobsters which had been kept in a commercial tidal pound constructed of creosoted timber contained highly elevated levels of benzo(*a*)pyrene and other carcinogenic hydrocarbons, including chrysene, benzo(*a*)anthracene, benzo(*b*)fluoranthene, dibenz(*a,h*)anthracene, and indeno(1,2,3-*cd*)pyrene. The maximum level of benzo(*a*)pyrene was 2300 ng/g wet weight in digestive gland, and 281 ng/g in edible tail meat. These levels are substantially higher than previously reported for any foodstuff, and are most probably attributable to creosote contamination during impoundment.

Key words: benzo(*a*)pyrene, polycyclic (polynuclear) aromatic hydrocarbon, carcinogen, seafood, lobster, shellfish, creosote

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Les auteurs ont procédé par chromatographie sur couches minces et par fluorescence pour déterminer si et dans quelle mesure des fruits de mer de commerce, frais et traités, renfermaient du benzo [*a*] pyrène, hydrocarbure aromatique polycyclique cancérogène. Ils n'en ont pas décelé dans les échantillons de poissons, sauf quand on leur avait ajouté de l'huile végétale (produits cancérogènes exogènes). La plupart des échantillons de mollusques et de crustacés en contenaient moins de 10 ng/g de poids frais, bien que parfois cette teneur pût s'élever jusqu'à 36 ng/g. Les échantillons de crabes et de crevettes en contenaient peu ou pas du tout (de la limite décelable jusqu'à 0,5 ng/g). Les homards de commerce en renfermaient de 0,8 à 7,9 ng/g. Dans ce cas, les auteurs ont poussé leurs recherches pour découvrir la source de contamination; ils ont employé la chromatographie en phase liquide à haute pression pour doser 13 isomères polycycliques. Chez les homards récemment capturés, la teneur en benzo [*a*] pyrène était inférieure à 1 ng/g. Ceux qui provenaient d'un parc à marée, construit en bois créosoté, en renfermaient de fortes quantités ainsi que d'autres hydrocarbures cancérogènes, notamment, du chrysène, du benzo [*a*] anthracène, du benzo [*b*] fluoranthène, du dibenz [*a, h*] pyrène et de l'indéno [1, 2, 3-*cd*] pyrène. La teneur maximale en benzo [*a*] pyrène a été de 2 300 ng/g de poids frais dans leurs glandes digestives et de 281 ng/g dans la chair comestible de leurs queues. Ces teneurs sont considérablement plus élevées que ce qui a été trouvé antérieurement dans des aliments, quels qu'ils fussent, situation sans doute attribuable à la contamination par le créosote durant le séjour en homarderie.

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POLYCYCLIC aromatic hydrocarbons (PAH) are present in some petroleum products, coal tar, urban air particulates, cigarette smoke, and in gasoline and diesel engine exhausts. These compounds may occur naturally (eg. crude oil), or be generated pyrolytically as the result of incomplete combustion in man-made or natural fires (National Academy of Sciences 1972). A number of polycyclic aromatic hydrocarbons, including the widely studied compound benzo(*a*)pyrene, are potent carcinogens in animals and man. PAH have been found in certain foods, where they may have resulted from external contamination by air pollutants, uptake from the soil, or generation during food processing by

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smoking or by high temperature cooking. The literature on the levels of PAH in different foodstuffs has been reviewed recently by Lo and Sandi (1978).

PAH carcinogens enter the marine environment from a variety of sources, including petroleum pollution, fallout from air pollution, effluents from industries and sewage treatment plants, storm drain runoff, and creosoted wharfs and pilings. Although there have been previous reports of the presence of PAH carcinogens in some seafoods, only a limited number of species from restricted areas of the world have been analyzed. Most analyses to date have been of noncommercial samples, often from areas suspected as being polluted. The extent to which commercial seafoods might be contaminated by PAH carcinogens is still largely unknown. In this study we report the results of the analysis of 22 species of fresh and processed commercial seafoods from 15 countries. In addition, we examine the possibility that commercial impoundment of lobsters in pens constructed of creosoted timber may contaminate this seafood with polycyclic aromatic hydrocarbons.

Materials and Methods

Samples

Except where noted, samples were obtained from local fish markets or specialty food stores. Fresh or fresh-frozen samples were frozen at −10°C until analysis. Fresh samples were drained of any fluid before analysis, while tinned samples were analyzed as a whole, including any packing oil or fluid. Samples are listed in tables under their common name, appearing on labels or product descriptions of commercial sources. Because many samples had undergone extensive processing, no attempt was made to identify the exact species involved. The country of origin noted in Table 1 refers to the best information available on the primary producer of the product (which in some cases is different from the processor). No smoked products were analyzed, as smoking is known to be an exogenous source of PAH contamination (Malanoski et al. 1968).

Extraction and Purification of Polycyclic Aromatic Hydrocarbons

Extraction and purification procedures have previously been described (Dunn 1976, 1979). In brief, samples were digested in alcohol and KOH, and then water added and the hydrocarbons partitioned into isooctane. Interfering materials were removed by column chromatography on Florisil®, followed by selective extraction of PAH into DMSO. Further interfering materials were removed by column chromatography on Sephadex LH-20, as described by Giger and Blumer (1974), except utilizing a solvent of toluene:ethanol (1:1) instead of benzene:methanol (1:1). An internal standard of radioactivity labelled benzo(*a*)pyrene was added to all samples before extraction to correct for losses during purification procedures.

Quantitation of Polycyclic Aromatic Hydrocarbons

Purified extracts from seafood samples (Table 1) were applied to cellulose acetate thin-layer chromatography plates, and the PAH compound benzo(*a*)pyrene isolated from other PAH isomers by chromatography using a solvent of toluene:ethanal:water (17:4:4) as described by Dunn (1976, 1979). Benzo(*a*)pyrene was quantitated by fluorimetry utilizing an artificial baseline technique to minimize the contribution of background fluorescence to the measured signal.

Extracts from lobsters (Tables 2, 3, and 4) were evaporated down into a small volume of DMSO, and then analyzed for 13 polycyclic aromatic hydrocarbon isomers by high pressure liquid chromatography. Aliquots of 2–10 μL were injected onto a reversed phase chromatography column (2.1 mm ID × 250 mm) packed with Perkin Elmer HC-ODS 10-μm adsorbent. Chromatography was at 30°C (with the column submerged in a water bath) and a flow rate of 0.5 mL/min. The solvent consisted of 60% acetonitrile, 40% water for 6 min, followed by a linear gradient of 3% per minute to 99% acetonitrile. PAH were detected by a variable wavelength UV absorption monitor at 296 nm (absorption maximum for benzo(*a*)pyrene), followed by a fluorescence monitor operating with a broad excitation band (340–380 nm, selected by a Corning 7-54 filter in series with a 7-60 filter), and measuring emission at wavelengths greater than 400 nm (selected by a Corning 3-73 U.V. cut-off filter, in series with a 4-76 red blocking filter to eliminate red leakage from the 7-54/7-60 excitation filter combustion). Solvents were air saturated, and a variable back pressure restrictor (Varian Associates) was used on the output line of the second detector to maintain an internal pressure of approximately 200 psi inside both detectors to suppress bubble formation. Each detector output was fed to a separate dual pen recorder, with one pen set at 10 times the sensitivity of the other pen to increase the dynamic range of chart recorder traces which could be easily measured.

Chromatographic peaks were identified by retention times, co-chromatography of reference compounds, and by the ratio in response between UV and fluorescence detectors. Peak areas were measured by triangulation, and the amount of injected component determined with the use of response factors prepared with reference compounds. The degree of contamination of the originally processed sample was calculated utilizing the calculated amount of material in an injection, the injected volume of sample, the recovery of material per unit volume of the injected sample (determined by measurement of the ^{3}H-benzo(*a*)pyrene internal standard), and the weight of the sample.

Results

Benzo(*a*)pyrene in Fresh and Processed Commercial Seafoods

Table 1 lists the levels of benzo(*a*)pyrene found in different samples, and in the case of tinned samples, the presence and type of any edible oil utilized in the packed product. Samples which contained benzo(*a*)pyrene (B(*a*)P) also contained other polycyclic aromatic hydrocarbons. These were visible as fluorescent bands on thin-layer chromatography plates, but were not quantitated in the present study. The majority of mollusk samples contained detectable B(*a*)P. Although most samples contained less than 10 ng/g wet weight, two samples contained more than 25 ng/g. Levels of B(*a*)P in most crustacean samples were lower than the

levels found in mollusks. Seven out of 12 samples of shrimp, prawns, and crab contained no detectable carcinogen (detection limit 0.1 ng/g) and with the exception of a single sample tinned with soya oil, levels of B(*a*)P were less than 0.3 ng/g. In contrast, levels of B(*a*)P ranging from 0.8 to 7.9 ng/g were found in the claw, tail, and leg meat of three lobster samples.

Levels of B(*a*)P on the order of 1–2 ng/g have been reported in soya and other vegetable oils, with some samples of oil containing no contamination (Grimmer and Hildebrandt 1967; Howard and Fazio 1969). Samples of vertebrate fish which were fresh or tinned without added oil did not contain detectable levels of carcinogen. In contrast, 5 of 7 samples packed in oil showed levels of B(*a*)P ranging from 0.2 to 2.6 ng/g. The data suggest that in the absence of added vegetable oil, vertebrate fish do not generally contain detectable levels of B(*a*)P, and that vegetable oils used in processing are a significant source of PAH carcinogens in tinned seafoods.

Since the failure to detect benzo(*a*)pyrene in vertebrate fish might simply reflect the relative cleanliness of the open ocean in which they were caught, an examination was made of B(*a*)P levels in noncommercial vertebrate fish taken from a harbour area in which mussels were contaminated to the extent of 5–10 ng B(*a*)P/g. No B(*a*)P (detection limit 0.02–0.2 ng/g) were detected in fillet and liver samples of lemon sole (*Parophrys vetulus*) and starry flounder (*Platichthys stellatus*). However, samples of fish stomach and intestine, including partially digested food, contained readily detectable amounts of B(*a*)P (about 1.0 ng/g), indicating that the fish were ingesting this carcinogen.

Polycyclic Aromatic Hydrocarbons in Lobsters

The levels of B(*a*)P found in lobsters (Table 1) were somewhat unexpected, in view of the fact that lobsters have been reported to metabolize this compound and excrete it as water soluble derivatives (unpublished work cited in Lee et al. 1976). The lobsters analyzed in Table 1 were from a retail fish store, and had been shipped live by an unidentified supplier in the Canadian Maritimes. In order to more fully explore the levels of PAH occurring in lobsters from Eastern Canada, we analyzed lobsters from a number of different areas.

Table 2 shows the levels of benzo(*a*)pyrene found in the tail meat of fresh caught lobsters. The levels found were uniformly low, with all samples containing less than 1 ng/g of benzo(*a*)pyrene. Levels of other polycyclic aromatic hydrocarbons, including the carcinogens benzo(*a*)anthracene, benzo(*b*)fluoranthene, dibenz(*a,h*)-anthracene, and indeno(1,2,3-*cd*)pyrene, were similarly low (ranging from nondetectable to up to approximately 5 times the benzo(*a*)pyrene level for benzo(*a*)-anthracene). Although there is considerable variability in the measured levels of benzo(*a*)pyrene in the samples, there is some suggestion that some sites yield lobsters with more contamination than those from other sites. Thus, all samples from Portuguese Cove contained at least 0.2 ng/g benzo(*a*)pyrene, whereas no more than a trace of benzo(*a*)pyrene was detected in four out of five samples from Brown's bank, and from the Eastern Passage, Halifax harbor. The low levels in the latter area are of special interest, as this area is in the proximity of two oil refineries, which might be expected to be a source of polycyclic aromatic hydrocarbons due to petroleum pollution.

The supply of fresh caught lobsters is very seasonal, and in order to have live lobsters available for the market year-round, lobsters are stored alive for periods of up to several months in tidal ponds. These consist generally of a shallow water area, often a bay or inlet, with a series of fences which form impoundment areas of up to several acres. Timber and fencing material used in the construction of the pounds is treated with creosote as a preservative. The practice of lobster impoundment has been reviewed by McLeese and Wilder (1964).

Creosote has been known to taint lobster flesh (McLeese and Wilder 1964, p. 27). Because creosote contains high levels of polycyclic aromatic hydrocarbons, the practice of storing live lobsters in pounds constructed of creosoted timber might contaminate this seafood with PAH carcinogens. We therefore examined the levels of PAH in lobsters before and after storage in a commercial tidal pound facility in New Brunswick, Canada. Table 3 shows the levels of benzo(*a*)pyrene in lobsters from a batch which was placed in the pound in early June 1978, compared with the levels in lobsters removed from the pound September 18, 1978 (approximately 3-mo storage). Levels in the tail meat of lobsters prior to impoundment averaged less than 1 ng/g, while after impoundment the average was 79 ng/g, with the most contaminated lobster containing 281 ng/g. Based on the analysis of lobster tissues reported in Table 1, the levels in the claw meat and leg meat would be expected to be of the same order as levels in the tail meat.

For three individual lobsters we also analyzed the digestive gland. This gland, popularly called the "tomalley" is eaten by a substantial number of people in the Maritimes, and is considered a delicacy. Levels of lipid are higher in this organ than in tail and claw meat, and the gland has been reported to selectively accumulate hydrophobic pollutants such as PCBs. Levels of polycyclic aromatic hydrocarbons in the digestive gland were, respectively 7, 8, and 11 times higher than the levels found in tail meat from the same individuals. The highest value recorded was 2300 ng/g, in a lobster whose tail meat contained 281 ng/g benzo(*a*)pyrene.

High pressure liquid chromatography indicated that other polycyclic aromatic hydrocarbons were also highly elevated in lobsters which had been impounded. The pattern of PAH isomers seen resembled closely the pattern seen in samples of commercial creosote, and extracts of creosoted wood. Table 4 shows the levels of some polycyclic aromatic hydrocarbons found in the edible tissues of a fresh caught and an impounded lob-

TABLE 1. Benzo(*a*)pyrene in commercial seafoods.

Species	Origin	Type[a]	B(*a*)P ng/g wet weight[b]
Mollusks			
Abalone	Canada	f	0.6
Clams	Canada	f	ND, 0.6, 0.6
	Italy	t	8.1
	Japan	t	ND, 5.6, 5.8, 6.3
	Korea	t	0.8
	Malaysia	t(v)	1.8
Cockels	England[c]	t	18, 19, 36
Cuttlefish	Spain	t(s)	0.2
Mussels	Canada	t	ND
	Denmark	t	3.3, 5.1
	England[c]	t	5.2, 5.3, 5.7, 25
	Germany	t(s)	1.6
	Spain	t(s)	2.0
Oysters	Canada	f	0.4, 1.6, 2.0, 3.2, 6.2
	Japan	t	0.7
Scallops	Canada	f	0.3
Squid	USA	t	ND, ND
	Spain	t(s)	1.0
Crustaceans			
Crab	Canada	f	ND, ND, ND, 0.2, 0.2, 0.3
	USA	t(s)	2.1
Lobster #1	Canada	f	claw: 3.8[d] tail: 7.9[d] legs: 5.1
Lobster #2	Canada	f	claw: 0.8[d] tail: 2.5[d]
Lobster #3	Canada	f	claw: 2.0[d] tail: 2.6[d]
Prawns	Canada	f	ND
	USA	f	ND
Shrimp	Canada	f	ND
	USA	t	ND
	Greenland	t	0.3
Vertebrate fish			
Arctic char	Canada	t	ND
Cod	Spain	t(s)	1.5
Cod liver	Germany	t	ND, ND
Dover sole	Canada	f	ND
Mackerel	Spain	t(s)	0.7
	Yugoslavia	t(v)	2.6
Salmon	Canada	f	ND
	Canada	t	ND
Sardines	Morocco	t(o)	0.2
	Norway	t(o)	ND
	Spain	t(s)	ND
Trout	Portugal	t(o)	1.4
Tuna	Japan	t	ND

[a]f = fresh or fresh-frozen, t = tinned or bottled, with soya (s), olive (o), or unspecified vegetable (v) oil.

[b]Multiple values for a species and country are for samples from different suppliers, unless otherwise noted. ND = less than 0.1 ng/g.

[c]Individual tins from the same supplier.

[d]Average of two determinations.

ster. Particularly noteworthy are the elevated levels of the carcinogens benzo(*a*)anthracene, benzo(*b*)fluoranthene, dibenz(*a,h*)anthracene, and ideno(1,2,3-*cd*)pyrene. Other polycyclic aromatic hydrocarbons which were detected, but not identified or quantitated in this study, were similarly elevated in impounded lobsters.

TABLE 2. Levels of benzo(*a*)pyrene in tail meat of fresh-caught lobsters from different areas.

Location	*n*	B(*a*)P, ng/g[a] wet weight
Portuguese Cove, near Halifax, N.S. (no obvious pollution sources)	4	0.2, 0.2, 0.3, 0.3
Northumberland Strait (no obvious pollution sources)	5	ND, tr., 0.4, 0.4, 0.5
Brown's Bank, N.S. ("offshore" lobsters from deep water)	5	tr., tr., tr., tr., 0.5
Eastern Passage, Halifax, N.S. (close to two oil refineries)	5	tr., tr., tr., tr., 0.4

[a]ND = not detectable, detection limit approximately 0.02 ng/g; tr. = trace, detectable on fluorescence detector, but not sufficient signal for accurate quantitation. Level below 0.1 ng/g.

TABLE 3. Levels of benzo(*a*)pyrene in tail meat of lobsters before and after impoundment.

Batch	*n*	B(*a*)P, ng/g wet weight	Mean
Commercial market lobsters of batch placed in impoundment early June 1978	5	0.4, 0.5, 0.5, 0.8, 0.9	0.6
Commercial market lobsters removed from impoundment September 18, 1978	10	7.4, 8.9, 23, 40, 43, 70, 75, 80, 161, 281	78.9

TABLE 4. Levels of polycyclic aromatic hydrocarbons in the tail meat of lobsters before and after impoundment.

Compound	U.S. EPA priority pollutant[a]	Carcinogenicity[b]	B(*a*)P, ng/g wet weight	
			Before	After
Phenanthrene	yes	−	32	100
Fluoranthene	yes	−	67	1815
Pyrene	yes	−	17.5	537
Triphenylene	no	−	5.1	627
Chrysene	yes	±	2.2	303
Benz(*a*)anthracene	yes	+	4.4	222
Benzo(*e*)pyrene	no	−	4.3	277
Benzo(*b*)fluoranthene	yes	++	1.1	261
Benzo(*k*)fluoranthene	yes	−	0.35	169
Benzo(*a*)pyrene	yes	+++	0.76	281
Benzo(*ghi*)perylene	yes	−	0.19	51
Dibenz(*ah*)anthracene	yes	+++	N.D.	153
Indeno(1,2,3-*cd*)pyrene	yes	+	0.54	137

[a]U.S. Environmental Protection Agency (1977).
[b]National Academy of Sciences (1972).

Discussion

The results suggest that PAH contamination of some seafood species is very widespread. Commercial and noncommercial oysters and clams (Cahnmann and Kuratsune 1957; ZoBell 1971; Fazio 1975; Guerrero et al. 1976; Panalacs 1976; Mix et al. 1977; Pancirov and Brown 1977) and noncommercial mussels (Dunn and Stich 1975, 1976; Dunn and Young 1976) have previously been reported to contain B(*a*)P and other PAH carcinogens. The levels found in these studies were generally less than 10 ng/g, but ranged up to 215 ng/g for noncommercial mussels growing in a creosote contaminated area (Dunn and Stich 1976). In the current study, commercial samples of these species also contained benzo(*a*)pyrene. In addition, we now report the presence of polycyclic aromatic hydrocarbons in cockels, abalone, scallops, lobster, crab, and shrimp.

As a group, mollusks appeared to be the most susceptible to contamination by polycyclic aromatic hydrocarbons. All shellfish species contained benzo(*a*)pyrene

in one or more samples. The contamination of commercial shellfish by benzo(*a*)pyrene appears to be widespread, as shellfish samples from nine countries in widely different parts of the world were involved. Crustaceans appeared also to be susceptible to contamination, although the levels found were very low except in the specific case of lobsters. In contrast to the contamination of shellfish, and crustaceans such as lobster, shrimp, and crab, there was no contamination of vertebrate fish except in cases where processed fish had been packed with vegetable oil. Since the contamination of vegetable oil with polycyclic aromatic hydrocarbons is well established (Grimmer and Hildebrandt 1967; Howard and Fazio 1969), contamination in this latter case most likely comes directly from the oil itself, and not from the seafood.

The levels of benzo(*a*)pyrene and related compounds found in marine organisms in the current study appear to be at least partially related to the ability of a species to metabolize polycyclic aromatic hydrocarbons. A variety of vertebrate fish have been reported to metabolize aromatic hydrocarbons, including benzo(*a*)pyrene (Payne 1977) and Lee and coworkers have shown that fish rapidly excrete benzo(*a*)pyrene as water soluble derivatives (Lee et al. 1972b). Rapid metabolism of PAH carcinogens by vertebrate fish would be expected to lead to low steady-state tissue levels of these compounds, and would account for the failure of the present study to demonstrate detectable levels of B(*a*)P in fillet and liver, even in fish from polluted areas. In contrast, bivalve mollusks have been reported to be unable to metabolize B(*a*)P (Lee et al. 1972a; Vandermuelen and Penrose 1978), and accumulated PAH are released only slowly (Lee 1977), probably by partitioning into water. This inability rapidly to clear aromatic hydrocarbons is reflected in the widespread contamination of bivalve mollusks by PAH, as reported in this and other studies.

Crabs and lobsters, but not amphipods or brine shrimp have been reported to have the capability of metabolizing benzo(*a*)pyrene (Payne 1977). These species have also been shown readily to excrete B(*a*)P as water soluble metabolites (Lee et al. 1976). However, in the current study, substantial levels of B(*a*)P were found in the edible tissues of lobsters, and low levels of carcinogen were found in a minority of shrimp and crab samples. This suggests that in comparison to vertebrate fish, either these crustaceans do not clear B(*a*)P as rapidly from their tissues, or their intake of B(*a*)P from the environment is substantially higher.

Highly elevated levels of polycyclic aromatic hydrocarbons were found in lobsters which had been impounded for a period of approximately three months in a commercial storage facility constructed of creosoted timbers. High pressure liquid chromatography of extracts of edible lobster meat revealed a pattern of PAH isomers very similar to that seen in commercial samples of creosote, and in extracts of creosoted timber. The data are consistent with direct contamination of lobsters with carcinogenic hydrocarbons derived from creosote.

There was considerable variability in the degree of contamination of lobsters from the same impounded lot. The origin of this variability is not clear, although it may be related to the fact that impounded lobsters tend to burrow in sediments, and remain relatively immobile (McLeese and Wilder 1964). Lobsters settling near creosoted timbers may accumulate higher levels of polycyclic aromatic hydrocarbons than those remaining in more remote areas of the impoundment facility.

Creosote contamination of marine organisms has previously been reported. Zechmeister and Koe (1952) isolated a number of PAH from thatched barnacles which had been growing on pilings which had received a surface creosoting 10 yr prior to sampling (Shimkin et al. 1951). The source of contamination was not positively identified, although it was noted that polycyclic aromatic hydrocarbons were absent in samples of the same species of barnacles taken from rocks. Zitko (1975) used a fluorescence fingerprinting technique to demonstrate creosote contamination of shellfish, and suggested that creosote contamination of coastal waters might be quite widespread. Dunn and Stich (1975, 1976) showed that groups of creosoted pilings are substantial point sources of PAH in the marine environment. Levels of benzo(*a*)pyrene in mussels were elevated within several hundred metres of wharf and dock areas, and gas chromatograms of polycyclic aromatic hydrocarbons isolated from mussels growing near creosoted pilings were similar to chromatograms of extracts of creosoted wood (Dunn and Stich 1976). Extracts of polycyclic aromatic hydrocarbons from barnacles growing on creosoted pilings have been shown to be carcinogenic in mice (Shimkin et al. 1951), and hyperplasia in an estuarine bryozoan growing on creosoted pilings has been attributed to coal tar creosote (Powell et al. 1970).

The degree of contamination of marine organisms in the vicinity of creosoted wood structures would be expected to depend on a number of factors. Besides the intrinsic ability of a species to take up and retain PAH, these include the amount of exposed wood surface, the rate at which PAH are leached from the surface, and the amount of tidal flushing or water currents in the area. Levels of contamination would be expected to be highest in areas with freshly creosoted timber and poor water circulation, and lowest with older weathered timber on exposed beaches. The variability introduced by such factors may account for the failure of Mix et al. (1977) to demonstrate a close relationship between levels of benzo(*a*)pyrene in shellfish and levels in surface samples of creosoted wood from the same area.

The potential for contamination of seafood by polycyclic aromatic hydrocarbons arising from chronic petroleum pollution or from oil spills is well recognized (Fazio 1975). However, the widespread contamination of commercial shellfish found in the current study suggests that carcinogen contamination of seafoods may

occur not only in such obviously polluted waters, but also in waters deemed suitable for commercial seafood production. The elevated levels of polycyclic aromatic hydrocarbons found in commercially impounded lobsters in addition point out that seafoods may potentially be contaminated by temporary holding facilities, and by aquaculture operations. The extensive use of creosote as a preservative for wooden structures may be a particular problem in this latter type of operation.

A substantial number of shellfish samples contained more than 5 ng/g B(*a*)P, with two samples containing more than 25 ng/g. The levels in these more contaminated shellfish samples are higher than the levels which have been generally found for smoked foods (Malanoski et al. 1968; Howard and Fazio 1969), and are on the same order as the levels which have been reported for charbroiled meats (Panalacs 1976; Howard and Fazio 1969; Lijinsky and Shubik 1964; Lijinsky and Ross 1967). In contrast to the situation with charbroiled meats, however, the consumption of PAH carcinogens from contaminated shellfish could be at least partly amenable to regulatory control. The wide variation in contamination levels found in individual shellfish samples of the same species suggests that the degree of contamination depends on the pollution in the location that the seafood has come from, as has been shown for noncommercial mussel samples (Dunn and Stich 1975, 1976). Appropriate shellfish sanitation standards could be utilized to remove shellfish from particularly contaminated areas from the marketplace.

Levels of benzo(*a*)pyrene and other polycyclic aromatic hydrocarbons found in fresh caught lobsters were comparable to the levels present in a number of common foods (Lo and Sandi 1978). However, levels of polycyclic aromatic hydrocarbons in lobsters which had been impounded are the highest values yet reported for any foodstuff, including heavily smoked meat products. The average level of benzo(*a*)pyrene found in impounded lobsters was 79 ng/g, compared with a typical contamination of charbroiled meats of approximately 10 ng/g (Lo and Sandi 1978). Similarly, the maximum levels of 2300 ng/g B(*a*)P in digestive and 281 ng/g in tail meat are substantially higher than the maximum levels of approximately 50 ng/g reported in heavily charred steaks. Further research is clearly needed to establish how typical these elevated levels of PAH are of impounded lobsters, and to investigate methods of reducing this form of exogenous contamination.

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Comparison of Fisheries Control Systems That Utilize Catch and Effort Data

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HILBORN, R. 1979. Comparison of fisheries control systems that utilize catch and effort data. J. Fish. Res. Board Can. 36: 1477–1489.

The relative merits of various methods for estimating the parameters of the Schaefer model from catch and effort data and of controlling the fishery are compared by simulation techniques. Estimation procedures compared are the linear and nonlinear methods for the discretized Schaefer model and Schnute's method for the continuous form of the Schaefer model. The control systems compared are feedback effort limitation, quota control for fixed escapement policies, and application of equilibrium effort. It is found that all estimation systems frequently fail to provide reasonable estimates of the Schaefer model and will produce poor catches, especially when managing long-lived, low productivity species. These estimation problems are most severe when the catch and effort data series begins after the stock has been heavily exploited. The failure of the estimation systems is primarily due to insufficient contrasts in the two independent variables of the multiple regression used for estimation, effort and catch per effort. The need for alternative policies that will explore the effort, catch per effort space is discussed. Application of the equilibrium effort may frequently be preferred to a fixed escapement policy; average catch may not be reduced, and variability in catch is much lower. Quota regulation is dangerous when the stock is heavily exploited and the biological parameters of the stock uncertain; at other times the quota method produces results comparable with effort limitation.

Key words: Schaefer model, feedback control, catch and effort, fisheries regulation, adaptive control

HILBORN, R. 1979. Comparison of fisheries control systems that utilize catch and effort data. J. Fish. Res. Board Can. 36: 1477–1489.

Des méthodes de simulation ont servi à comparer les mérites relatifs de diverses techniques d'estimation des paramètres du modèle de Schaefer à partir de données sur la capture et l'effort, et de régulation de la pêcherie. La comparaison se fait entre les méthodes linéaire et non linéaire pour le modèle disjonctif de Schaefer et la méthode de Schnute pour la forme continue de ce même modèle. Pour ce qui est des systèmes de régulation, nous comparons la limitation de l'effort rétroactif, la régulation des contingents dans l'élaboration de politiques touchant à l'échappement d'un nombre déterminé de poissons à la capture et, enfin, l'application d'un effort d'équilibre. Nous constatons que tous les systèmes d'estimation sont souvent impuissants à fournir des estimations raisonables du modèle de Schaefer et aboutissent à de maigres captures; surtout quand il s'agit de gérer des espèces longivives et à faible productivité. Ces problèmes d'estimation sont le plus sérieux quand la série de données sur capture et effort commence après que le stock ait été lourdement exploité. La cause première de l'échec des systèmes d'estimation est l'insuffisance des contrastes entre les deux variables indépendantes de la régression multiple utilisée dans l'estimation, soit effort et capture par unité d'effort. Nous examinons la nécessité de politiques de rechange qui exploreront effort et capture par unité d'effort. On préférera souvent l'application d'un effort d'équilibre plutôt qu'une politique d'échappement fixe de poissons; la capture moyenne ne serait pas pour cela réduite et la variabilité de la capture serait beaucoup plus faible. Le contingentement est une mesure dangereuse quand le stock est lourdement exploité et que ses paramètres biologiques sont incertains; en d'autre temps, le contingentement donne des résultats comparables à la limitation de l'effort.

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FISHERY management is widely recognized to be a problem in optimal control. The accepted method of calculating optimal fishing policies is to specify a simple model of the fishery dynamics, and then calculate by mathematical analysis or numerical methods the optimal policy to meet some specified objective (Goh 1961; Reed 1974; Clark 1976; Walters 1975; Hilborn 1976; Walters and Hilborn 1976; Beddington and May 1977; Reed 1978; Walters and Hilborn 1978). Unfortunately, models used for calculation of optimal management policies are necessarily simplifications of the real fishery

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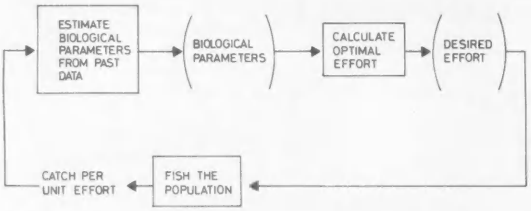

FIG. 1. Integration of a biomass pool model into a fishery decision making process using feedback estimation and control.

dynamics, and one must assume that the optimal policies derived for these models will be near optimal for the real fishery.

Many fisheries are managed on the basis of historical data on effort and total catch; these time series are used to make inferences about the productivity parameters of the fish stock and its current size. Figure 1 shows how catch and effort data can be used in an integrated management system. Past data on catch and effort are used to calculate parameters and stock size. The biological parameters and stock size are used to calculate the optimal effort or catch; the fishery occurs under these regulations and another catch and effort data point is generated and the analysis repeated for the next year. The major purpose of this paper is to examine the performance of various "optimal" control strategies that have been proposed in the literature.

Alternatives to catch and effort analysis do exist and are widely used in real fisheries. When age at catch can be determined, virtual population estimation or cohort analysis is widely used (Ricker 1975). Such methods can be used to estimate the parameters and state of the system, and may provide considerably more insight than total catch and effort data. In some fisheries larval sampling programs or echo sounding studies may also provide valuable clues about the stock condition. In this paper I will not attempt to test the utility of these methods, but will confine myself to the use of catch and effort data.

Methods

How can one compare alternative methods of fishery control? Ideally we would test proposed methods on a number of fisheries with several replicates of each method. We would naturally want to test each proposed method on different types of fish (slow growing vs. fast growing, pelagic vs. benthic, etc.). Unfortunately, it is not practical to experiment in this way. The cost to society of a poor method would be high, and there are few good opportunities for replication in the real world. Given the high levels of variability in fisheries production, a large number of replicates would be required. Possible exceptions are freshwater lakes where dozens of similar fisheries may exist, and good controlled experiments might be possible.

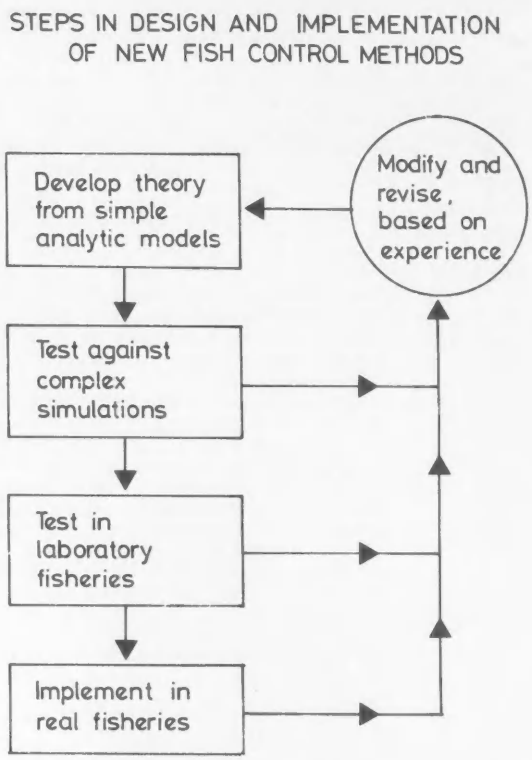
STEPS IN DESIGN AND IMPLEMENTATION OF NEW FISH CONTROL METHODS
Develop theory from simple analytic models
Modify and revise, based on experience
Test against complex simulations
Test in laboratory fisheries
Implement in real fisheries

FIG. 2. Steps in the design, testing, and implementation of a new fishery control method.

A Design for Testing

Given our inability to test newly developed methods of fishery control in real world fisheries, I propose a four step procedure for examining such methods. These four steps are shown in Fig. 2. First is the development of the methods via whatever procedures — be they sophisticated mathematics or pure wizardry. The second step involves application of the methods to realistic computer simulation models of fish populations to find strengths and weaknesses in the control systems. The third step — in theory to be used only on those methods that do well in harvesting simulation models of fish populations — is laboratory testing. Laboratory populations should, in principle, provide a better test than simulated populations because the researcher need not build all the biological assumptions into his computer — the fish should have them ingrained genetically. Such laboratory experiments should serve to eliminate many proposed methods by subjecting them to some of the wide variety of nature's tricks that real fishery managers face. The fourth and final step is implementation of the methods on real fisheries. We must recognize that this last step will not be done within the context of the scientific method. It will not be possible to conduct good trial experiments where a new method is introduced, but we can perhaps test its performance statistically against an earlier method.

Ricker's (1958) work on control of fish populations was one of the earliest attempts to examine fishing policies on simulated populations. Southward (1968) modelled the Pacific halibut stocks, the fleet and the management system, and compared the sensitivity of total yield to biological assumptions and management schemes. Silliman and Gutsell (1958) have fished laboratory populations of guppies experimentally, thereby pioneering the concept of using laboratory populations to test understanding of harvested population dynamics.

In this paper, I describe the second step of testing the control methods on simulated populations. Since it is not possible to test all control systems or biological assumptions, I hope primarily to develop some general results that can be thoroughly tested on specific models appropriate to particular fisheries.

Testing Against Simulated Populations

Theory underlying present management includes simple descriptions of dynamics of real fish populations. Therefore, in these tests the theoretical control algorithms manage simulated populations whose dynamics are more complex than the models for which the algorithms have been shown to be optimal. This is effectively the approach Southward (1968) used, except he was concerned with testing alternatives only for Pacific halibut, whereas I am concerned with general management procedures. To further enhance the realism of these experiments, stochastic variation is easily introduced at points within the simulation models.

I constructed models to describe in detail the annual change of a fish populations in response to exploitation. Various control systems described below harvest this population by controlling fishing effort. Catch-per-unit-effort is monitored by the control systems. The simulated population has age structure, density dependent recruitment, and several noise terms, but the control system uses only catch and effort data. Each simulation begins with 5 yrs of moderate effort to provide a set of "historical data." The control methods use past data to estimate parameters, the current population size, and, finally, the desired harvest for the next period. After the control system specifies the effort, or quota, the simulation model generates "actual" catch and stock changes for the next fishing interval (Fig. 3).

I ran each control method for 50 simulated fishing years. The sum of annual catches and remaining population is the index of performance: the higher the index, the better the performance. It is necessary to add on the remaining population so that there is no premium on catching all the fish in the last interval. On the other hand, this implies no penalty for leaving the stock fished to a low level.

Alternative Management Procedures

Estimation procedures — A commonly used model for catch–effort analysis of fish population dynamics is the Schaefer model. Although Schaefer originally wrote it as a differential equation (Schaefer 1957), it is frequently used as the following difference equation (Walters and Hilborn 1976; Uhler 1978).

$$(1)\quad N_{t+1} = N_t + N_t r\left(1 - \frac{N_t}{k}\right) - C_t$$

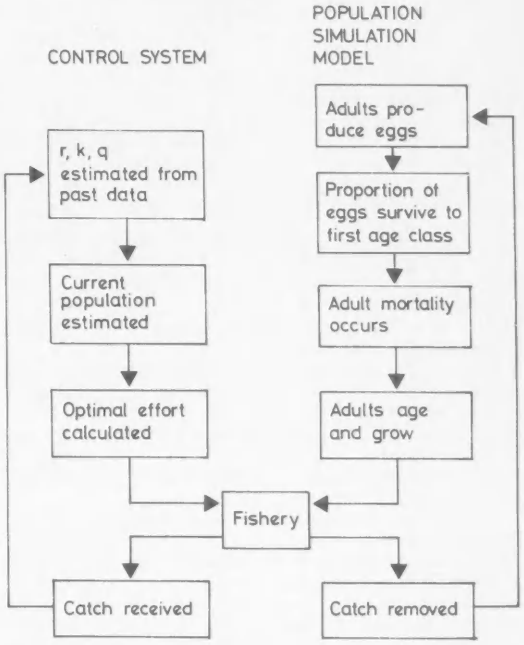

FIG. 3. Flow diagram of the control system and population simulation model used in testing alternative control systems.

where: N_{t+1} = population at time $t + 1$
N_t = population at time t
r = growth parameter
k = unfished equilibrium population size
C_t = catch at time t

If we specify C_t as:

$$(2)\quad C_t = N_t E_t q$$

where: E_t = fishing effort at time t
q = proportion of fish stock caught per unit fishing effort,

then equations 1 and 2 can be transformed into a linear regression of the form:

$$(3)\quad \left(\frac{\frac{C_{t+1}}{E_{t+1}}}{\frac{C_t}{E_t}}\right) - 1 = r - \frac{r}{qk}\left(\frac{C_t}{E_t}\right) - qE_t$$

Given a time series of C_t's and E_t's, the best estimates of r, k, and q can be obtained from equation 3. Although the C_t's are not independent as assumed in multiple regression theory, it is well established in control theory (Gelb 1974) that equation 3 is not far from an "optimal estimator." From the estimates of r, k, and q, N_{t+1} can be predicted and the regulations for the next fishing season calculated.

A serious problem with equation 2 is that for any q, a high effort level can generate a catch greater than the

population. An alternative assumption is that there is a short fishing season during which there is no natural mortality, and that the instantaneous rate of catch is proportional to the effort and population size. The important feature of this exponential catch equation is that noninstantaneous catch per unit of effort goes down with increasing efforts. Under these conditions (Ricker 1975) we have:

$$(4)\quad C_t = N_t(1 - e^{-q'E_t})$$

where: q' = a catch coefficient reflecting the instantaneous catching power of a unit of effort.

Note that as E_t approaches zero, q' approaches q. Unfortunately the combination of equations 1 and 4 cannot be written as a linear regression and must be solved by nonlinear estimation methods.

Schnute (1977) has solved the continuous form of the Schaefer model, and derived an approximate linear regression estimation procedure that is relatively simple to calculate. This method does not assume a short fishing season. Uhler (1978) has compared the reliability of estimation procedure for the Schaefer model and found that methods like Schnute's are preferred to equation 3.

In this paper I will compare the performance of three estimation procedures.

1) Linearized difference equation version of the Schaefer model given in equation 3.
2) Difference equation version of the Schaefer model with the saturating catch function, equation 4.
3) Schnute's method of solving for the parameters of the continuous Schaefer model (Schnute 1977, equations 40–41).

Control procedures — Many methods are used to regulate fisheries; seasonal closures, gear restrictions, and quotas are common. The major difference between methods is whether the effort will be restricted or a catch quota will be set.

It has been shown (Schaefer 1957; Clark 1976) for the Schaefer type models that the maximum sustained yield can be achieved using the so-called "bang–bang" or "fixed escapement" policies that maintain the population at its point of maximum production. If the population is below this level, harvesting is stopped until it recovers; if the population is above this level, the harvest is set to drive the population down to the optimum as fast as possible.

Using equation 2, N_t can be estimated as

$$(5)\quad \hat{N}_t = \frac{C_t}{qE_t}$$

From this $\hat{N}_t$, via equation 1, $\hat{N}_{t+1}$ can be predicted. The optimum population size N^* is $k/2$. Therefore, the desired catch (C_d) under a fixed escapement policy is:

$$(6)\quad \begin{aligned} C_d &= \hat{N}_{t+1} - N^* \quad \text{if} \quad \hat{N}_{t+1} > N^* \\ C_d &= 0 \qquad\qquad\quad \text{if} \quad \hat{N}_{t+1} \le N^* \end{aligned}$$

If we use a quota system, then we simply set the quota to be C_d. However for an effort limitation policy the desired effort E_d must be estimated, by either

$$(7)\quad \text{eqn. 2: } E_d = \frac{C_d}{q\hat{N}_{t+1}}$$

TABLE 1. Estimation/control systems tested. Methods 1 and 2 require perfect information a priori, and are used only as baselines for comparison of other policies. They are not in any way practical management alternatives.

1. Perfect information, fixed escapement
2. Perfect information, constant effort
3. Linear estimation, fixed escapement effort regulation (equations 3 and 7)
4. Nonlinear estimation, fixed escapement effort regulation (equations 1, 4, and 8)
5. Nonlinear estimation, fixed escapement, quota (equations 1, 4, and 6)
6. Schnute estimation, fixed escapement effort regulation (Schnute 1977)
7. Schnute estimation, equilibrium effort regulation (Schnute 1977, equation 22)

$$(8)\quad \text{or eqn. 4: } E_d = \frac{\ln\left(1 - \dfrac{C_d}{\hat{N}_{t+1}}\right)}{q'}$$

An alternative to fixed escapement is to apply the optimal equilibrium effort which Schnute (1977, eq. 22) showed is estimated by

$$(9)\quad E_e = \frac{r}{2q}$$

There also corresponds the maximum equilibrium catch C_e which can be easily calculated. The application of equilibrium catch or effort (C_e, E_e) will lead to a gradual return towards the equilibrium N^*. Application of fixed escapement catch or effort (C_d, E_d) leads to a more rapid return towards N^*.

Thus for any estimation procedure there are at least four possible control procedures, a fixed escapement quota (C_d), a fixed escapement effort (E_d), an equilibrium quota (C_e), and an equilibrium effort (E_e). Table 1 summarizes the estimation/control system tested in this paper.

Baselines for Comparison

Ideally we would like to compare the results of a particular management system against the best possible management. The best approximation I know is to apply a fixed escapement policy where the optimal escapement is known a priori. I accomplish this by numerically testing which escapement level produced the best yield from the simulation model, using the criteria described earlier. This control system was given the true population size at each time period; thus it had perfect information about optimal escapement beforehand, and had perfect real time information about current population size.

An alternative to fixed escapement is constant effort, where the optimum effort is known a priori. I derived the optimal effort numerically by running the simulation model with different fixed effort levels to find the best effort level.

Structure of the Fish Population Models

I wished to compare the performance of alternative

estimation and control systems with a wide variety of population types. I therefore constructed two extreme simulations. Model A represents a long-lived, slow growing species that does not mature until 4 yr of age, and whose net increment in population biomass is largely derived from adult growth. Model B represents a species with high natural mortality rates where the fish mature in their first year and do not grow thereafter. Thus all population increment is due to recruitment.

The following model captures the attributes of Model A in a parsimonious way by assuming age-independent natural mortality rate and a Beverton-Holt stock recruitment relationship. Model B is identical with the exceptions noted above.

$$N_{t,t+1} = N_{t-1,t}s$$

$$w_t = ai$$

$$z_t = \sum_{t=4}^{20} N_t f_t$$

$$f_t = \begin{cases} 0 & \text{if } w_t < w_T \\ (w_t - w_T)d & \text{if } w_t > w_T \end{cases} \tag{11}$$

$$N_{1,t} = \frac{mz_t}{(h + z_t)} e^v$$

where: $N_{i,t}$ = number of fishes in the ith age-class at time t
s = adult survival rate from natural losses excluding fishing
w_t = weight of individual fishes at age i
w_T = individual weight threshold below which no eggs are produced
a = kg of body weight gained per year by individual fish
z_t = total eggs produced in year t by all adults
d = number of eggs per kg of body weight $> w_T$
f_t = number of eggs produced per animal age i
$N_{1,t}$ = number of eggs surviving first year
m = maximum of N_1 when $v = 0$
h = number of eggs for N_1 to equal $m/2$ when $v = 0$
v = normal random variable with a mean of 0.0 and a standard deviation of σ_v

Fishing mortality is assumed to be a function of fishing effort and I assumed that all age-classes are equally vulnerable. Assuming a very short fishing season with no natural mortality, the exponential catch equation is used:

$$C = P(1 - e^{-qEw}) \tag{7}$$

where: C = catch in kg
P = population size in kg
E = fishing effort
q = catch coefficient
w = a normally distributed random variable with a mean of 1 and standard deviation of σ_w

Behavior of the Population Models

The solid line in Fig. 4 shows the relationship between population size in kg and the production over a wide range of stock sizes for Model A. This was derived by arbitrary application of effort required to direct the stock slowly over a large range of stock sizes. While this population model has a behavior similar to the Schaefer model, the models are not identical since (1) the age structure in my model will "remember" past management actions, and (2) net population productivity will not be exactly a quadratic curve in relation to total stock as assumed by the Schaefer model. When variability is added to the simulations by making $\sigma_w = 0.2$, the scattered production points in Fig. 4 result.

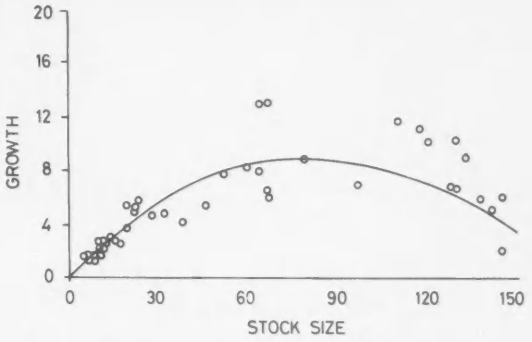

FIG. 4. The relationship between net population increase (in weight) and the population size (in weight) for Model A. The solid line represents a deterministic model at stable age distribution. The dots represent the observed net increase when the stock is driven from high to low densities and then let recover.

The characteristics of the fish in Model B are:

1) Fish grow to 1 kg in their first year and cease to grow thereafter,
2) adult mortality is 50% per year,
3) fish first reproduce in their second year,
4) all fish two years or older are equally fecund.

The relationship between stock size and productivity for this population is shown in Fig. 5. The solid line represents the stock production relationship with no variability, and the points represent "observed" values when $\sigma_w = 0.2$. There is little relationship between stock size and productivity when the stock size is greater than 10. Table 2 shows the parameter values used in Models A and B.

Comparisons Made

In using simulation results, care must be taken to assure that the results are not critically dependent upon starting conditions or parameters. First, I identified three key starting conditions that represent different conditions of a fishery:

1) Starting with the unexploited stock,
2) Starting with a stock near maximum sustained yield equilibrium,
3) Starting with a heavily overfished stock.

Second, I tested the sensitivity to two of the key parameters in Model A, adult survival rate from cases other than fishing, s ($s = 0.6, 0.7, 0.9$) and the fecundity per unit body weight d ($d = 10, 20, 40$). It was found that the starting conditions were very important, and the parameter sensitivity relatively unimportant, so I repeated the starting condition experiments with Model B.

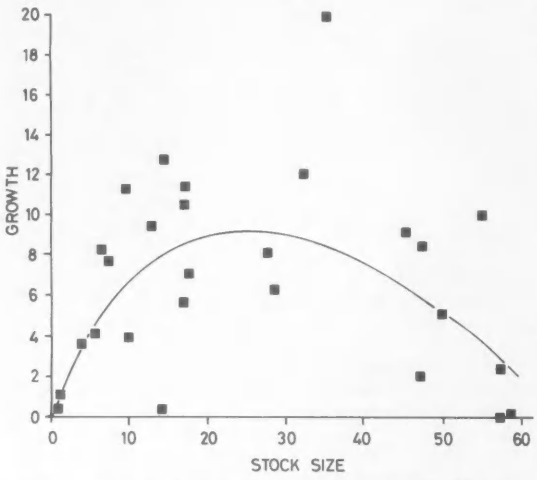

FIG. 5. The relationship between net population increase (in weight) and the population size (in weight) for Model B. The solid line represents a deterministic model at stable age distribution. The squares represent the observed net increase when the stock is driven from high to low densities and then let recover.

SIMULATION METHOD

Each simulation began with 5 yr of alternate years of low and medium effort. At the end of the 5 yr the time series of catch and effort was made available to the control system. If the control system was unable to estimate positive parameters, a default effort of 20 was used. Twenty units of effort was chosen somewhat arbitrarily. It is higher than the equilibrium effort and would cause an unexploited stock to be reduced to 20–30% of its unexploited level. I used nine different random number sequences, the same nine sequences were used for each control option tested.

Results

Table 3 shows the results of one run of each estimation/control system using Model A, basic parameters, starting with an unfished population. The total catch is the catch during 50 yr of exploitation, minus the difference between starting stock size and the final stock size. The first estimation/control system (perfect information with fixed escapement policy) always generates the best total catch, and the catch of all other estimation/control systems are divided by the best catch (using the same random number sequence) to arrive at the percent of maximum catch. The final column is the coefficient of variation of the catch.

The Schnute estimation system with fixed escapement failed to estimate positive parameter values in this test; this often happened with the linear model as well. Frequently a random number sequence that caused any estimation procedure to fail would cause most of the linear procedures to fail and would cause the nonlinear procedures to estimate very poor parameter values. However, the nonlinear procedures always estimated positive parameters; these estimates could be utilized in a control procedure and are included in the results presented.

TABLE 2. The parameter values used for Model A and Model B.

Parameter	Model A	Model B
s	0.7	0.5
w_T	3	none
a	1	1 in first year no subsequent growth
d	20	20
m	20	40
h	300	150
σ_w	0.2	0.2
σ_v	0.2	0.2
Age at first reproduction	4	1

PARAMETER SENSITIVITIES

The sensitivity of the results was tested using three random number sequences for higher and lower fecundity and higher and lower adult survival rates.

TABLE 3. The results of exploiting Model A from unharvested conditions. The percent of maximum catch is calculated by dividing the catch obtained by each estimation/control system by the catch obtained by the perfect information, fixed escapement system.

Estimation/control system	Total catch	% of maximum catch	Coefficient of variation of catch
Perfect information, fixed escapement	390	100	.77
Perfect information, constant effort (optimum fixed effort)	390	100	.32
Linear estimation, fixed escapement effort control	271	69	1.22
Nonlinear estimation, fixed escapement effort control	387	99	.81
Nonlinear estimation, fixed escapement, quota control	382	98	.55
Schnute estimation fixed escapement effort regulation	unable to obtain positive parameters	—	—
Schnute estimation, equilibrium effort regulation	362	93	.73

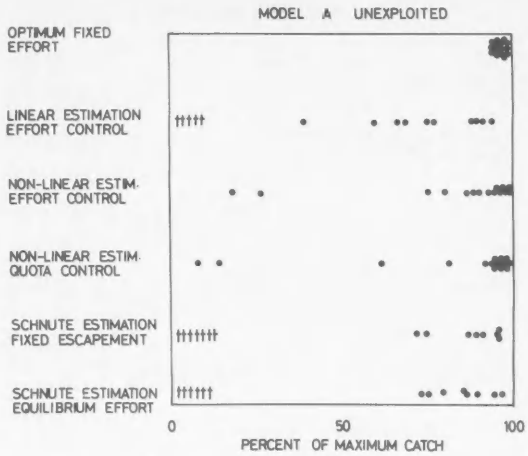

FIG. 6. The outcomes of 15 different 50-yr runs of each estimation control system for Model A, starting with an unexploited population. Percent of maximum yield is the catch for the particular run divided by the catch obtained by the perfect-information–fixed-escapement control system using the same random number sequence. Daggers represent cases where the estimation system was unable to estimate positive parameters.

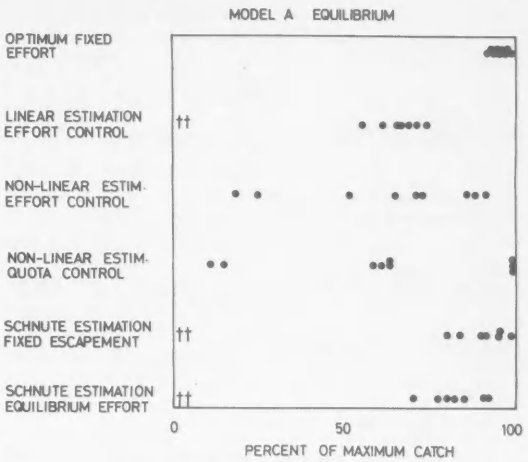

FIG. 7. The outcomes of nine different 50-yr runs of each estimation control system for Model A, starting near MSY equilibrium conditions. Percent of maximum yield is the catch for the particular run divided by the catch obtained by the perfect information, fixed escapement control system using the same random number sequence. Daggers represent cases where the estimation system was unable to estimate positive parameters.

There was no clear effect of the changes in parameters upon the results, especially in comparison to the dramatic effect of the starting conditions. I therefore report only all the results of the parameter sensitivities under Model A, unfished starting conditions.

MODEL A

Unexploited stock — Figure 6 shows the percent of maximum harvest obtained for each control system managing Model A starting from unexploited conditions. Note that perfect information fixed escapement does not appear on this figure since its value is already 100%. Each dot represents one 50-yr run of the particular control system. Daggers represent a failure of the estimation system to obtain positive parameters for use in the control system. The fifteen points for each control system represent three runs of each of the parameter combinations described above and three runs of "normal" parameters. It is clear that the preferred policy is either the perfect-information-fixed-escapement, or perfect-information-fixed-effort. Since these are not viable management alternatives, I will mention them only as baselines. The estimation systems using a linear model (the two utilizing the Schnute method and the nonintegrated linear model) very frequently fail to estimate positive parameters. (If any parameter was negative, the default effort of 20 units was applied.) However, when they do estimate positive parameters, they perform very well. The two methods utilizing the nonlinear estimation model generally performed very well, but occasionally became locked into a bad set of parameter estimates and seriously mismanaged the stocks.

Equilibrium stocks — Figure 7 shows the results of nine random number sequences of Model A starting from a stock size at equilibrium near the maximum sustained yield. The linear models were much more successful at obtaining positive parameter estimates from this starting condition than from unfished stocks. The two methods utilizing the Schnute method obtained excellent results when they estimated positive parameters. The general performance of the other methods was not as good as starting with an unexploited stock. The declining catch per effort that one obtains when starting from an unexploited stock provides valuable information to the non-Schnute methods, and when deprived of this information by starting from equilibrium conditions, these estimation control systems are less effective. The quota system occasionally does very poorly, and occasionally does very well.

Overexploited stocks — Figure 8 shows the results of nine runs of each control system starting with a population that was heavily overexploited. The general performance of all estimation control systems was very poor, they usually failed to recognize that the stock was overexploited and did not allow it to recover to its more productive levels. The linear models had great difficulties in obtaining positive parameter estimates, but when the Schnute method did obtain positive parameter esti-

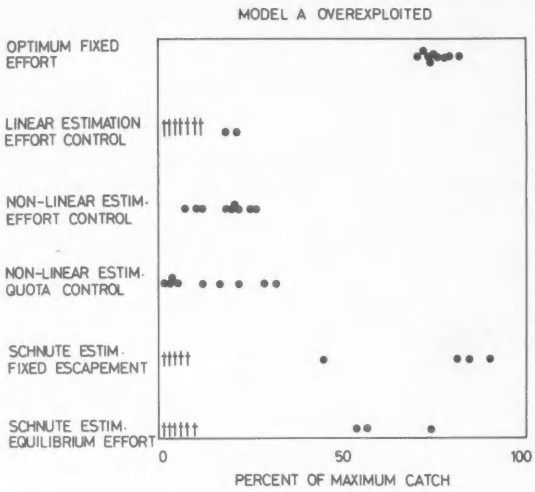

FIG. 8. The outcomes of nine different 50-yr runs of each estimation control system for Model A, starting with an overexploited population. Percent of maximum yield is the catch for the particular run divided by the catch obtained by the perfect-information–fixed-escapement control system using the same random number sequence. Daggers represent cases where the estimation system was unable to estimate positive parameters.

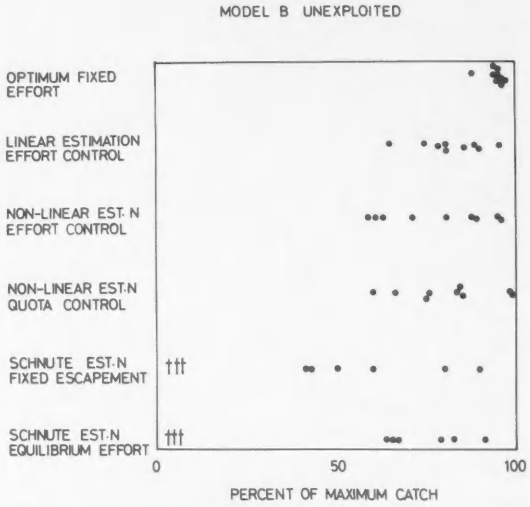

FIG. 9. The outcomes of nine different 50-yr runs of each estimation control system for Model B, starting with an unexploited population. Percent of maximum yield is the catch for the particular run divided by the catch obtained by the perfect-information–fixed-escapement control system using the same random number sequence. Daggers represent cases where the estimation system was unable to estimate positive parameters.

mates, it recognized that the stock was overexploited and allowed it to recover. The Schnute method with fixed escapement performed better than the Schnute method with equilibrium effort, because even after the equilibrium effort system recognized the stock was overexploited, it did not shut down the fishery to let the stock recover as fast as possible.

MODEL B

The major difference between Model A and Model B was the high productivity of Model B. This allowed an overexploited stock to recover in a few years and meant that the natural variation in the system would send the estimation control system over a relatively wide range of stock sizes.

Unexploited stocks — Figure 9 shows the results of nine runs of each control system from an unexploited state. As in Model A the general performance was good, but there were two major differences. The linear estimation procedures had less problems with estimating negative parameters, and the nonlinear estimation system did not get locked into poor parameter estimates.

Equilibrium stocks — Figure 10 shows the results of starting with Model B stock near the MSY equilibrium. This appears to differ little from starting from the unfished stock, probably because the stock is pro-

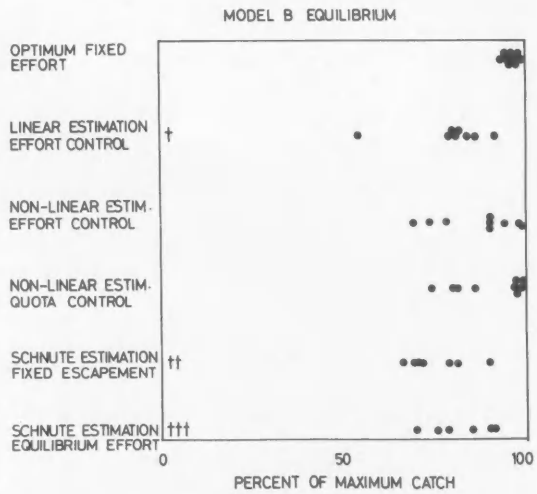

FIG. 10. The outcomes of nine different 50-yr runs of each estimation control system for Model B, starting near MSY equilibrium conditions. Percent of maximum yield is the catch for the particular run divided by the catch obtained by the perfect-information–fixed-escapement control system using the same random number sequence. Daggers represent cases where the estimation system was unable to estimate positive parameters.

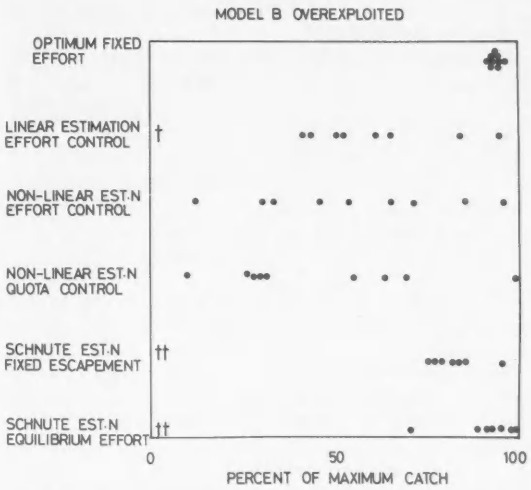

FIG. 11. The outcomes of nine different 50-yr runs of each estimation control system for Model B, starting with an overexploited population. Percent of maximum yield is the catch for the particular run divided by the catch obtained by the perfect-information–fixed-escapement control system using the same random number sequence. Daggers represent cases where the estimation system was unable to estimate positive parameters.

ductive enough to move to its unfished equilibrium in 1 or 2 yr, so there is effectively little difference between equilibrium and unfished stocks.

Overfished stocks — Figure 11 shows the results of starting with seriously overexploited stocks. The yields are lower than the two previous cases with Model B, but there were only a few cases of keeping the stock very low and not recognizing it was overexploited. The quota system seemed to be the most likely to make serious errors; the low points for the quota system represent cases where it nearly wiped out the stock in the early years of management by setting the quota nearly as the real total population size. The Schnute method is quite interesting, because except when it failed to get positive parameter estimates, it performed very well, considerably better than it did for unexploited or equilibrium stocks.

Table 4 presents the results of Fig. 6–11 as average percent of maximum catch, average coefficient of variation of the catch, (in parentheses) and the number of times the estimation system failed to produce positive parameter estimates over the number of times that estimation system was tried for that combination of starting conditions and models (in square brackets).

The coefficient of variation shows no real surprises. The perfect information/constant effort policy has the lowest coefficient of variation and the Schnute method with equilibrium effort is next lowest. The quota system has a relatively high coefficient of variation, but this was expected since it was being applied in a fixed escapement policy.

Discussion

Comparison of Estimation/Control Systems

Perfect information/constant effort — This system performed within 6% of maximum in all cases except Model A starting at overexploited conditions. In that case the constant effort policy did not allow the population to rapidly recover to its productive level and some overall catch was lost. The fast growing Model B fish did recover rapidly from overexploitation under this policy, and we can conclude that given information about the biological potential of a stock, a constant effort policy should work well except when a slow reproducing stock is in an overexploited state. Beddington and May (1977) and Reed (1978) have suggested that nonfeedback policies are probably undesirable for managing populations given environmental unpredictability. The results presented above suggest that this is probably true, but for another reason. The need for feedbacks are due more to the need to incorporate information as it becomes available than the need to rapidly respond to stock fluctuations due to environmental variability. Given good information, feedback policies may not be as important as previously thought.

Linear model/effort limitation — This estimation system proved to have serious problems in finding positive parameters with Model A. It is interesting that this failure occurred primarily with Model A starting from high or low populations levels, but not from equilibrium. The general problem of failure of estimation systems will be discussed separately for all systems. The overall performance of this estimation/control system was no better than the nonlinear model, and since the nonlinear model did not have the problem with negative parameters, it is the preferable one.

Non-linear estimation/effort limitation — The most interesting feature of this system is the contrast between how well it worked for Model A unexploited, how the yield was reduced when starting at equilibrium, and its terrible failures when starting from low levels. The difference was not as severe in Model B, probably because the high productivity and noise of Model B pushed the system over a wider range of stock sizes. It seems likely that when starting from an unexploited stock, the control system sees a declining catch per effort as the stock is reduced towards MSY, and that this information helps provide good estimates of appropriate levels of effort. When the system starts near MSY it does not see the long decline in catch per effort and makes more mistakes, and when the system starts with an overexploited stock it simply has no way of knowing that by reducing effort it would get a greatly increased yield. This case corresponds almost exactly

TABLE 4. Summary of the average yields, coefficients of variation (in parenthesis) and number of times the estimation system failed to provide positive parameter estimates (in brackets) for the runs described in the text.

	Model A			Model B		
	Unfished	Equilibrium	Overfished	Unfished	Equilibrium	Overfished
Perfect information, fixed escapement	100 (0.90)	100 (0.48)	100 (0.80)	100 (0.64)	100 (0.62)	100 (0.64)
Perfect information, constant effort (optimum fixed effort)	99 (0.48)	95 (0.28)	77 (0.51)	95 (0.33)	97 (0.32)	95 (0.34)
Linear estimation, fixed escapement effort control	75 (1.14) [5/15]	64 (0.92) [1/9]	25 (0.59) [5/9]	82 (1.05)	80 (1.15) [1/9]	62 (0.89) [1/9]
Nonlinear estimation, fixed escapement effort control	82 (1.14)	64 (1.08)	18 (1.10)	78 (0.62)	85 (0.69)	55 (0.73)
Nonlinear estimation, fixed escapement, quota	85 (0.90)	64 (1.34)	15 (2.38)	84 (0.54)	93 (0.53)	45 (0.96)
Schnute estimation, fixed escapement effort regulation	88 (1.06) [8/15]	90 (0.82) [2/9]	75 (1.12) [5/9]	60 (0.98) [3/9]	75 (0.84) [2/9]	82 (0.78) [2/9]
Schnute estimation, equilibrium effort regulation	85 (0.81) [7/15]	86 (0.50) [2/9]	61 (0.50) [6/9]	74 (0.62) [3/9]	83 (0.47) [3/9]	90 (0.42) [2/9]

with the type of problem presented by Walters and Hilborn (1976, Fig. 5) for a salmon type stock and recruitment estimation problem. However, the estimation of biological parameters from catch and effort data is much more complex than from stock and recruitment data. Smith (1979) has shown that the normal feedback control policies (Walters and Hilborn 1978) will provide near optimal results for stock recruitment type systems; the results in this paper suggest that when the complexity of estimating parameters from catch and effort data are added, the problem posed by Walters and Hilborn (1976) becomes much more severe, and standard optimal control procedures fail.

Another disturbing feature of this estimation/control system is that the time sequence of efforts is highly variable. The fixed escapement policy leads to many years of low catch, which may be quite undesirable in a real fishery.

Nonlinear estimation/quota control — The general performance of this system was quite similar to the effort limitation system described above. The major difference occurred when starting from low population levels. The quota system has the danger that the quota may be set equal to or greater than the stock size in a given year, which will lead to near extinction of the stock. Many of the very low yield points on Figs. 8 and 11 resulted from this problem. I conclude that the quota system is probably only dangerous when there is large uncertainty about stock levels and the stock is actually at low levels.

Schnute estimation/fixed escapement — The Schnute system is particularly interesting from two points of view. The two systems incorporating Schnute's estimation procedure were clearly the best methods *when they could estimate the parameters.* Unfortunately they frequently failed to find positive parameters. The performance of this system when starting from Model A, overfished, where the nonlinear estimation procedures failed so badly, is impressive. The estimation procedure recognized the stock was overexploited and let it recover, something the nonlinear estimation procedures failed to do. It is not clear how dependent this result is on the nature of the fish model being managed. Since the system did well with both Model A and Model B, I suspect that this conclusion is general.

Schnute estimation/equilibrium effort — The performance of this system was similar to the fixed escapement policy described above, except that the coefficient of variation in catch was lower, and it did not let the Model A overexploited stock recover as fast as the fixed escapement policy. Fixed escapement policies appear to provide little improvement over more constant effort policies, and given the social desirability of more constant catches, more emphasis should be placed on such policies (see Walters 1975).

CAUSE OF FAILURES

The failure of the linear estimation systems to find positive parameter estimates, and the failure of the nonlinear estimation systems to perform well when starting from low population levels, suggest that there are serious deficiencies in using catch and effort data to manage fish populations. There are three reasons

why these failures may have occurred:

1) The default control options chosen when negative parameter estimates were obtained kept the system about a relatively constant condition that provided no information.
2) The failure was due to very particular interactions between the estimation system and the model being managed.
3) The failure was due to some general problems associated with estimating the parameters of biomass pool models from complex age structured populations.

I believe that reasons 1 and 2 can be rejected. The default effort level for the linear estimation systems was sufficient to drive the population from high densities to levels well below the MSY level. Yet nearly half the time Model A was started at high levels, the linear estimation procedures failed.

Explanation 2 can be rejected because I was using three separate estimation systems and they all failed at some time. Model A was more prone to failure than Model B, presumably because the high productivity and noise in Model B provided a more informative set of natural perturbations. However, failures did occur with both models and all three estimation systems. This strongly suggests that failure is not due to peculiarities in the estimation system, but is a more general property.

Thus failures are probably due to the general structure of estimating the parameters of a Schaefer type model from data on a complex age structured population. This can be broken into two possibilities; either the Schaefer model is fundamentally inappropriate to use on data from age structured populations, or else there is a general problem of estimating its parameters from data.

From equation 3 we can see that the two independent variables in the estimation equation are the effort and catch per effort. From regression theory we know that there must be a contrast in the independent variables in order to resolve uncertainty about the regression coefficient, i.e. the independent variables must not be strongly correlated. Any policy that fails to generate contrasts between catch per effort and effort will be prone to failure due to poor parameter estimation. To test this possibility, I designed an "adaptive probing policy." Starting with Model A, unexploited conditions, I applied 4 yr of low effort, then 6 yr of high effort to drive the stock to near MSY, and then 4 yr of low effort to let it recover again. I then used these data as starting conditions for the Schnute method. In ten runs of this scheme the Schnute method never failed to get positive parameter estimates, and produced 98% of the maximum yield, in spite of the 4 yr of low effort at the beginning and another 4 later on. Therefore, all of the estimation failures observed for the Schnute method, and presumably for the other linear methods can be ascribed to a lack of contrast between catch per effort and effort, *and not to the Schaefer model being too simple.*

Similar policies work for stocks starting at overexploited conditions; the stock must be allowed to recover to near MSY, and then exploited again. This further demonstrates that the problem is not that the Schaefer model is inappropriate for these more complex fish population models, but that it requires observing the stock over a wide variety of sizes. Further, the stock must not only pass through a wide range of stock sizes (which will be reflected in catch per effort), but must also be allowed both a recovery and an exploitation phase. The recovery allows estimation of rate growth (r), while the other phase establishes the scaling between population size and catching power (k vs. q).

Figure 12 illustrates the need for contrast between effort and catch per effort. To find good parameter estimates, it is necessary that the tilted plane be accurately defined by contrasting points across it. The two independent variables of the regression, E_t and $(C/E)_t$ are the two axes on the horizontal plane, the dependent variable is shown on the z axis. The intercept on the z axis is the "r" parameter. The slope along the E_t axis is "$-q$," the slope along the $(C/E)_t$ axis is "$-r/qk$." The multiple regression fits the plane in this three dimensional space that minimizes the sum of squared deviations between the plane and the observed data.

Figure 12 shows several fisheries development trajectories in this sample space. Trajectory A represents the type of failure that occurred with the linear methods when starting from unfished populations. The fishery started with moderate effort, and pushed the stock below MSY, but never estimated realistic parameters. From Fig. 12 we can see it would have a good estimate of $-r/qk$, but this is not sufficient to determine any single parameter, or to decide upon appropriate levels of effort. An infinite series of planes could be fit to the line represented by trajectory A.

Starting with an overfished stock, and maintaining low effort to let the stock recover is illustrated by trajectory B. This trajectory is more informative, "r" can be estimated as can r/qk, but the uncertainty about k and q means uncertainty about appropriate management policies. We can, however, estimate the optimal equilibrium catch per effort from this trajectory. The catch per effort at MSY equilibrium for equation 3 is half of the catch per effort at unfished equilibrium which is kq. Thus $kq/2$ is the optimal equilibrium catch per effort, but the level of effort required to achieve this catch per effort remains uncertain from trajectory B.

Trajectory C represents a typical fishery development. Effort gradually increases, and catch per effort decreases. From this development trajectory none of the parameters can be estimated.

Southward (1968) noted that the International Pacific Halibut Commission had found estimation of Schaefer model parameters from catch and effort data produced unrealistic parameters, a result very much like the estimation failures observed in my simulations. Figure 12 illustrates why this happens and how it can

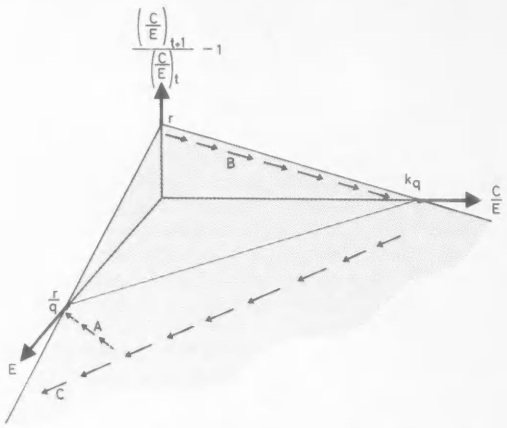

FIG. 12. A three dimensional representation of the multiple regression plane for estimating the discrete form of the Schaefer model (equation 3). The two axes in the horizontal plane, catch per effort and effort, represent the independent variables of the multiple regression. Variable on the vertical plane is the dependent variable of the multiple regression. The least squares procedure chooses the plane that minimizes the sum of squares between the plane and the observed data points. Trajectory A represents a fishery starting unexploited and driven rapidly below MSY. Trajectory B represents a fishery starting from overexploited state and recovering. Trajectory C represents a normal fishery development scenario: an unexploited stock is gradually driven down by increasing effort. All of these trajectories provide information along a single line in the effort, catch per effort plane, and thus no contrast between the independent variables. Without this contrast an infinite number of planes can be fitted to the data points, and no reliable estimates of the parameters are possible.

be avoided. From trajectories A or C, a few years of low effort would provide contrasting data and good estimates; from trajectory B a few years of high effort would provide the contrasts. It should be possible, for any given type of fish population, to calculate the needed length of such experimental probes to provide management with good estimates of the biological parameters.

THE ROLE OF ADAPTIVE MANAGEMENT

Walters and Hilborn (1976, 1978) have suggested that it may be desirable to use "actively adaptive" approaches that involve deliberate perturbations to provide information. Recent work by Smith (1979) has shown that, for stock and recruitment models, active adaptive approaches provide improvement over normal feedback control only when historical stock data have been collected mostly near MSY. The results in this paper show that using only catch and effort data, normal feedback control is at best going to produce 80–90% of the maximum harvest, and with slow growing stocks starting at low conditions it may produce only 15–20% of maximum harvest. It seems likely that active perturbations to provide information will have great payoffs.

Recent advances in application of active adaptive control theory (Smith 1979) have overcome the major technical impasses discussed in our previous papers on adaptive control. It appears likely that some formal adaptive algorithms may be developed in the near future for use in estimating Schaefer type models for catch and effort data.

Alternatives to the formal algorithms are heuristic experimental management designs described by Walters and Hilborn (1976, 1978). Formal integration of these designs into a testing routine as described in this paper would be very useful. We now know that there are serious deficiencies in normal feedback estimation and control systems and that these deficiencies are particularly common when exploiting unproductive stocks that are overfished.

ALTERNATIVES TO ADAPTIVE MANAGEMENT

Throughout the discussion in this paper it has been assumed that the only information available to the control system is a time series of catch and effort; this is rarely the case. Consider the case where the estimation systems were least successful, i.e. when they were faced with an overexploited stock and no historical data on preexploitation conditions. Although such situations may occur (Fraser River sockeye, Walters and Hilborn 1976), there are usually at least some indications that the stock used to be at higher levels. This information may take the form of historical catch data without reliable effort data, or simply weak indications that there used to be a much larger stock. The failures of the control systems in these circumstances were due to their inability to recognize from the catch and effort data that the stock was overexploited. A real manager can use this other type of information to conclude that there is a good possibility that the stock is overexploited and to adopt appropriate regulations in spite of the analysis of his catch and effort data. There is an important need to integrate softer data with the harder catch and effort statistics.

Many fisheries use the age structure of the catch to estimate natural mortality rates and past recruitment histories. Although these techniques are not applicable to all fisheries, they may prove to prevent estimation control systems from making large errors. It would be possible to test an estimation control system based upon age structured catch analysis against the same type of models I tested in this paper.

Biological information on the state of the stock can be obtained by sampling programs in some fisheries. This provides additional information that can be used to determine if the stock is underexploited, near MSY, or overexploited. There is a need for formal methods to incorporate this type of information into manage-

ment systems primarily dependent upon catch and effort data.

Future Directions

This paper has pointed out the pitfalls in the current theory for optimal utilization of catch and effort data. I see three major directions for future research. First, detailed studies must be made to understand why the estimation procedures fail so often. It is not sufficient to say that there is insufficient contrast between catch per effort and effort; guidelines need to be developed as to the minimum contrast needed.

Second, I have only tested methods that use total catch and effort data. It is not at all clear whether methods utilizing catch at age data would improve the performance of management systems. These methods need to be tested against models similar to those I used. Finally, actively adaptive methods, both formal and heuristic, need to be developed and tested.

Conclusions

1) Estimating the parameters of a Schaefer model and applying optimal feedback control has serious drawbacks if historical catch and effort data do not reflect a wide range of catch per effort and efforts.
2) These problems are most serious when good data collection begins after the stock is heavily exploited.
3) Quota limitations can produce serious overexploitation and occasional stock extinction if applied when the stock is well below MSY and the biological parameters are uncertain.
4) Applying equilibrium effort generates catches comparable with those from a fixed escapement policy in all circumstances except when managing a low productivity stock that is initially overexploited.

Acknowledgments

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On Representing the Length Dependence of Acoustic Target Strengths of Fish

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FOOTE, K. G. 1979. On representing the length dependence of acoustic target strengths of fish. J. Fish. Res. Board Can. 36: 1490–1496.

The problem of representing the length dependence of acoustic target strengths of fish is addressed by studying the legitimacy of merging target strengths that are inhomogeneous in species or frequency. The target strengths are of two kinds: maximum and averaged dorsal aspect target strengths, which are derived from measurements of gadoid target strength functions of three species at two ultrasonic frequencies. The target strengths are expressed variously according to unnormalized, wavelength-normalized and length-normalized schemes. Overall coincidences and coincidences of slopes among simple linear regressions of target strength on fish length, when segregated by target strength type and manner of representation, are investigated through analysis of covariance. Examination of computed significance levels demonstrates that merging of target strengths in species or frequency is generally unjustified and that no one representation method is superior to another in facilitating the merging of such data. The unnormalized representation is to be preferred when merging is justified because of its simplicity and avoidance of the frequency bias inherent in the normalized representations. The hypothesis of scaling of target strengths is refuted.

Key words: target strength, regression, covariance analysis, fish abundance estimation

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L'auteur voit s'il peut représenter la longueur des poissons en fonction de l'intensité des échos de diverses espèces à différentes fréquences. Les intensités d'échos donnent la configuration dorsale maximale et moyenne des poissons, établie d'après les fonctions d'intensité d'échos de trois espèces de gades, à deux fréquences ultrasoniques. Ces intensités sont exprimées par des diagrammes non normalisés, aux longueurs d'ondes normalisées et aux longueurs de poisson normalisées. L'ensemble des coïncidences et celles des pentes de simples régressions linéaires de l'intensité des échos sur la longueur des poissons, groupées par type d'intensité d'échos et par mode de représentation, sont soumises à une analyse de la covariance. L'examen des seuils calculés de signification montre que la combinaison d'intensité d'échos de diverses espèces à différentes fréquences est généralement sans valeur et qu'aucun mode de représentation n'est supérieur à un autre pour combiner ces données. Quand cette combinaison est valide, la faveur va à la représentation non normalisée en raison de sa simplicité et parce qu'on évite les erreurs systématiques de fréquence que comportent les représentations normalisées. L'hypothèse de la mise à l'échelle des intensités d'échos est rejetée.

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THERE are three basic representations of the length dependence of fish target strengths in the literature. These are represented by Haslett's "universal diagram" (Haslett 1965), Love's wavelength-normalized representation (Love 1969), and the simpler, unnormalized target strength-to-fish length representation (Nakken and Olsen 1977).

In Haslett's "universal diagram," or length-normalized representation, the backscattering cross section is normalized to the square of fish length and plotted against the fish length-to-acoustic wavelength ratio. Two advantages of the representation are that deviations of the pertinent cross section from a pure quadratic length dependence for data that are gathered at the same frequency are easily seen and that the variability of the data is easily gauged. Examples of uses of the representation are found in Haslett (1965, 1977) and Love (1969, 1971).

In the wavelength-normalized representation of target strengths the backscattering cross section is normalized to the square of the acoustic wavelength and plotted against the length-to-wavelength ratio. An advantage of the representation, which it shares with the length-

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normalized representation, is the ease with which it frequently enables data gathered on fish of disparate lengths at disparate frequencies to be presented on the same graph, as when the length-to-wavelength ratio is limited to a rather narrow interval. The range from 1 to 100 is of particular interest in applications of derived regressions to the acoustic estimation of fish abundance at high frequencies. Examples of uses of the wavelength-normalized representation scheme, which was introduced by Love in 1969, are contained in Love (1969, 1971, 1977), McCartney and Stubbs (1971), Shibata (1971), and Goddard and Welsby (1979).

The third-mentioned representation of target strength data ignores normalization. Data are expressed simply as backscattering cross sections and plotted against fish length. Examples of this unnormalized representation are contained in Midttun and Hoff (1962), Cushing et al. (1963), Yudanov et al. (1966), Nakken and Olsen (1977), and Yudanov (1977).

The attractions of the unnormalized representation are its simplicity and avoidance of the frequency bias which generally arises in the two normalized representation schemes. Merging of data gathered on fish of widely varying lengths at widely varying frequencies is discouraged. This may not be counted a disadvantage, however, because the scaling hypothesis implicit to the two normalized representations has not been demonstrated. According to this hypothesis the scattering cross sections of fish of different lengths are simple functions of the length-to-wavelength ratio. In particular, any given scattering cross section is assumed to have a definite power law dependence on the length-to-wavelength ratio. The coefficient of proportionality in this relationship is assumed to have a generally slight, but deterministic frequency dependence.

In each of the three representation schemes numerous target strength data are often condensed by means of a least mean squares regression analysis of the logarithmically transformed cross section, with or without normalization, on the logarithm of fish length variable. For target strength data which are homogeneous in frequency content the regression analyses are equivalent in the three representations. For data of inhomogeneous frequency content the resultant regressions are generally different.

The question naturally arises as to which of the three representation schemes is best. A related, more fundamental question is whether or not target strength data which are inhomogeneous in species and/or frequency content can legitimately be merged, i.e. whether or not the data are essentially the same. The resolution of these questions is the aim of this paper.

The two questions are addressed by studying the statistical significance of coincidences among regressions established for certain target strength data when expressed according to the three representation schemes. The target strength data are of two kinds: maximum and averaged dorsal aspect target strengths. These are derived from measurements of the dorsal aspect target strength functions of gadoids of three species at two ultrasonic frequencies, by extraction and computation (Foote 1979a, b), respectively. Data of a given kind of derivation are merged separately with respect to frequency and species and together with respect to both characteristics. The compatibility or apparent homogeneity of various data, thence legitimacy of merging, is determined by observing the magnitudes of the computed significance levels. The original question of which representation scheme is best is answered by comparing corresponding significance levels.

Materials and Methods

The maximum and averaged dorsal aspect target strengths, which are fundamental to the regression analyses of this study, are derived from the gadoid dorsal aspect target strength functions measured by Nakken and Olsen (1977) and edited in Foote and Nakken (1978). The numbers and length ranges of the species- and frequency-discriminated functions of that study which are used here are presented in Table 1.

The maximum dorsal aspect target strengths extracted from the described measurements are presented in the format of the unnormalized representation scheme in Fig. 1. The content of the scatter diagrams of the figure is similar, but not identical to that of comparable scatter diagrams presented in Nakken and Olsen (1977). This reflects the effect of editing the data of the earlier study by purging excessively noisy or saturation-limited measurements, as described in Foote and Nakken (1978). The precise length distribution of each of the six data sets may be inferred from the respective scatter diagram of Fig. 1.

The target strength data of the scatter diagrams are regressed linearly on fish length according to the equation

$$(1)\quad \mathrm{TS} = \hat{m} \log \ell + \hat{b}$$

where TS, in this context, denotes the maximum dorsal

TABLE 1. Numbers of gadoid specimens and length ranges represented by measured dorsal aspect target strength functions used in computations.

Species	Frequency = 38 kHz		Frequency = 120 kHz	
	Number of specimens	Length range (cm)	Number of specimens	Length range (cm)
Cod (*Gadus morhua*)	68	6.7–96.0	44	6.7–67.0
Saithe (*Pollachius virens*)	59	9.1–68.0	48	9.1–68.0
Pollack (*Pollachius pollachius*)	44	19.7–61.0	39	19.7–52.0

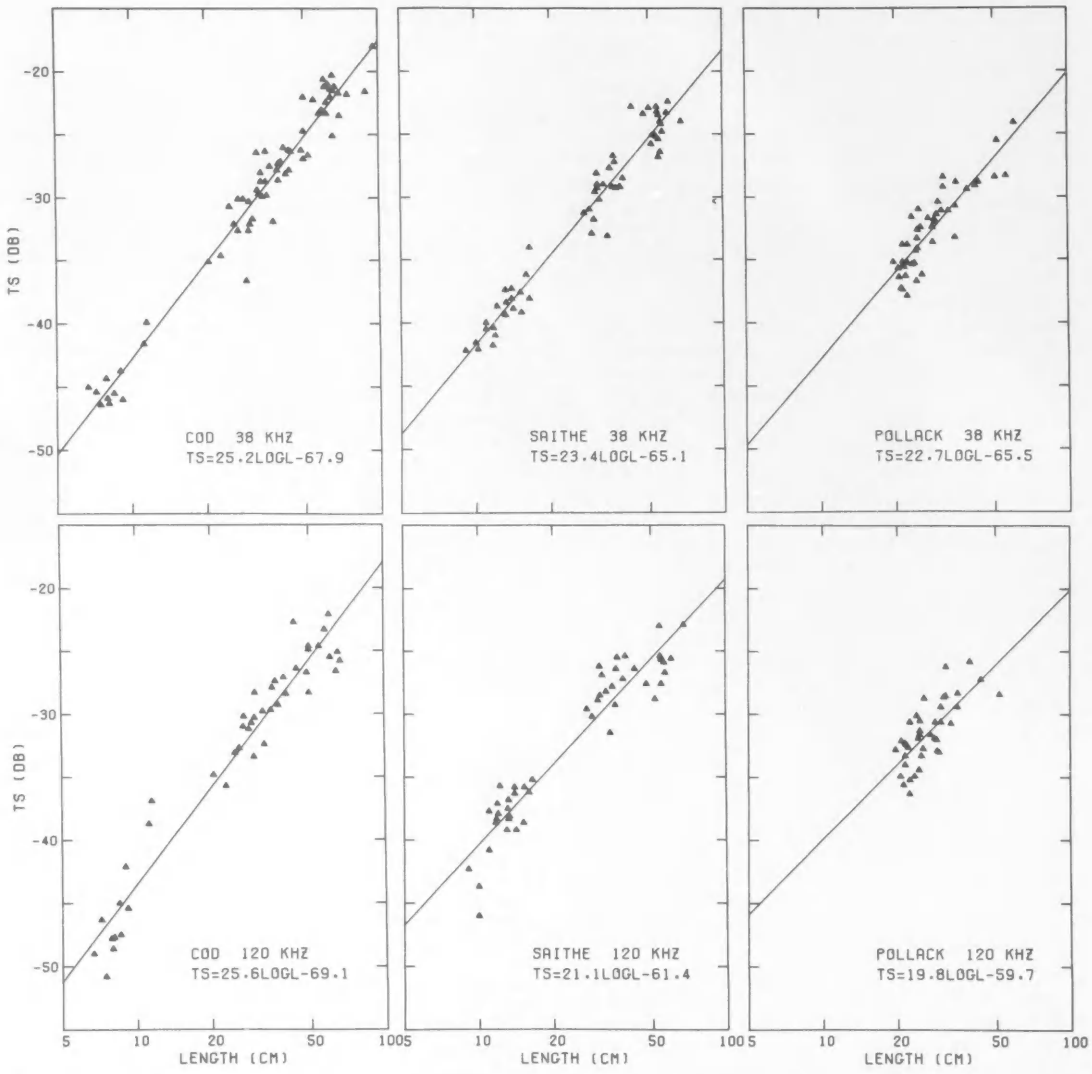

FIG. 1. Scatter diagrams with linear regression equations of maximum dorsal aspect target strength TS, expressed in units of decibels, on fish length for three gadoid species at two ultrasonic frequencies.

aspect target strength and ℓ, the fish length when expressed in centimetres. The regression coefficients $\hat{m}$ and $\hat{b}$ are written with circumflexes to indicate their validity with respect to a finite data sample. The regression analyses are summarized in Table 2. There the provisional nature of the coefficients is expressed quantitatively through estimates of the corresponding standard errors, denoted est[SE($\hat{m}$)] and est[SE($\hat{b}$)]. The standard error of regression, SE, and correlation coefficient, ρ, are also computed.

Expression of the regression analyses of the same data in the two normalized representation schemes may be obtained directly by comparing expressions of the regression equations in the normalized formats with equation (1) when interpreted by the definition of target strength in terms of the backscattering cross section σ; viz.

$$(2)\quad \mathrm{TS} \equiv 10 \log \frac{\sigma}{4\pi}$$

In this equation σ is expressed in units of square metres and TS in units of decibels, such that the target strength of an idealized perfectly reflecting sphere of radius 2 m is

TABLE 2. Summary of regression analyses of maximum dorsal aspect target strengths on fish length for three gadoid species at two ultrasonic frequencies.

Species	Frequency (kHz)	$\hat{m}$	est[SE($\hat{m}$)]	$\hat{b}$	est[SE($\hat{b}$)]	SE	ρ	est[SE($\hat{b}_1$)]	ρ_2
Cod	38	25.2	0.6	−67.9	1.0	1.6	0.979	0.6	0.701
Cod	120	25.6	1.0	−69.1	1.4	2.1	0.969	1.4	0.652
Saithe	38	23.4	0.7	−65.1	1.0	1.4	0.976	0.6	0.553
Saithe	120	21.1	1.0	−61.4	1.4	1.9	0.951	1.3	0.157
Pollack	38	22.7	1.9	−65.5	2.8	1.6	0.879	1.6	0.213
Pollack	120	19.8	3.0	−59.7	4.3	1.8	0.737	4.0	−0.012

0 dB. The regression equations in the wavelength- and length-normalized representation schemes are, respectively,

$$(3)\quad 10 \log \frac{\sigma}{\lambda^2} = \hat{m}_1 \log \frac{\ell}{\lambda} + \hat{b}_1$$

and

$$(4)\quad 10 \log \frac{\sigma}{\ell^2} = \hat{m}_2 \log \frac{\ell}{\lambda} + \hat{b}_2$$

where λ is the acoustic wavelength and σ, ℓ, and λ are expressed in consistent units. Thus, for the case of data that are homogeneous in frequency, the regression coefficients of equations (3) and (4) are related to those of equation (1) by the equations

$$(5a)\quad \hat{m}_1 = \hat{m}$$

$$(5b)\quad \hat{b}_1 = \hat{b} + (\hat{m} - 20) \log \lambda + 10 \log 4\pi + 40$$

$$(6a)\quad \hat{m}_2 = \hat{m} - 20$$

$$(6b)\quad \hat{b}_2 = \hat{b} + (\hat{m} - 20) \log \lambda + 10 \log 4\pi + 40$$

where λ is expressed in centimetres. The factor of 40 arises because of the expression of ℓ in equation (1) in units of centimetres and the need to express σ in equation (2) in units of square metres. The estimated standard errors of regression coefficients $\hat{m}_1$ and $\hat{m}_2$ are identical to est[SE($\hat{m}$)]. The estimated standard errors of regression coefficients $\hat{b}_1$ and $\hat{b}_2$ are identical and generally different from est[SE($\hat{b}$)]. The standard errors of the regressions are identical in the three representations. The correlation coefficients of data in unnormalized and wavelength-normalized representations are identical and considerably different from the correlation coefficient of length-normalized data. For the present interesting case of backscattering cross sections at ultrasonic frequencies, the correlation coefficient of data expressed according to the length-normalized representation scheme is generally small in magnitude because of the approximately quadratic length dependence of cross section in this length-to-wavelength regime. The two quantities, est[SE(b_1)] and ρ_2, which cannot be inferred simply from the regression analysis of data expressed in the unnormalized format, are included in Table 2.

Averaged dorsal aspect target strengths, which compose the second part of the derived data base, are discussed briefly in Foote (1979a, b). In general, an averaged target strength, denoted <TS>, is defined in terms of the averaged backscattering cross section $<\sigma>$ by analogy with equation (2):

$$<\text{TS}> \equiv 10 \log \frac{<\sigma>}{4\pi}$$

where $<\sigma>$ is defined as the average of the corresponding backscattering cross section with respect to the beam patterns of observing sonar and spatial and orientation distribution of observed fish. For definiteness a particular model of observation of fish by a directional downward-looking sonar is considered. The transmit and receive beam patterns are assumed to be identical to that of an ideal circular piston of half-beamwidth 2.5 degrees. The spatial distribution is assumed to be uniform, which does not exclude the important geometry of horizontal layers by virtue of the assumed downward orientation and directivity of sonar beam. The fish orientation distribution is assumed to be of the type observed by Olsen (1971); namely, an essentially normal distribution in tilt angle. The tilt angle is defined as the angle between the fish centerline, or imaginary straight line running from the root of the tail to the tip of the upper jaw, and horizontal plane, with the sign convention that positive tilt angles denote head-up positions. The tilt angle distribution is defined precisely as a normal distribution which is truncated for tilt angles departing from the mean by more than three standard deviations.

Averaged dorsal aspect target strengths are computed for the measured gadoid data described above for two particular realizations of the model. In these the mean and standard deviation pairs are (−4.4, 16) and (0, 5) degrees. The first pair of parameters represents the actual observations of Olsen (1971). The second pair of parameters is intended to describe another, more tightly aligned fish aggregation or school. Results of regressing the averaged target strengths on fish length are presented in Tables 3 and 4 for the two sets of distribution parameters. Deduction of corresponding characteristics of regression analyses in the normalized representation schemes may be effected as in the case of regression analyses of maximum dorsal aspect target strengths.

The legitimacy of simple linear regression analysis of the derived target strength data when discriminated by frequency, species, type, and manner of representation is accepted. Inspection of scatter diagrams of maximum and averaged dorsal aspect target strengths, which are presented in Fig. 1 and in Foote (1979a, b), respectively, suggests the reasonableness of the hypothesis of homoscedasticity or homogeneity of variance of the data. Application of Barlett's test (Pearson and Hartley 1966) to the standard errors of the regression analyses described in Tables 2 and 3, when segregated by target strength type, supports this hypothesis. The apparent heterogeneity of variance among data of Table 4 may be overlooked apropos of the remarks of Zar (1974) on the inefficiency of Bartlett's test and the robustness of analysis of variance. Thus, in at least two cases, and arguably in the third case too, analysis of covariance may be applied to determine whether coin-

TABLE 3. Summary of regression analyses of averaged dorsal aspect target strengths on fish length for averaging with respect to a sonar of half-beamwidth 2.5 degrees and fish tilt angle distribution with parameters (−4.4, 16) degrees for three gadoid species at two ultrasonic frequencies.

Species	Frequency (kHz)	$\hat{m}$	est[SE($\hat{m}$)]	$\hat{b}$	est[SE($\hat{b}$)]	SE	ρ	est[SE($\hat{b}_1$)]	ρ_2
Cod	38	21.9	0.6	−68.3	0.9	1.4	0.979	0.6	0.375
Cod	120	23.9	0.7	−73.7	1.0	1.4	0.984	0.9	0.666
Saithe	38	20.4	0.5	−66.7	0.8	1.0	0.983	0.4	0.115
Saithe	120	19.8	0.7	−68.0	1.0	1.4	0.971	1.0	−0.043
Pollack	38	19.1	1.5	−66.3	2.2	1.3	0.886	1.3	−0.092
Pollack	120	15.0	2.8	−61.7	4.0	1.6	0.658	3.8	−0.279

TABLE 4. Summary of regression analyses of averaged dorsal aspect target strengths on fish length for averaging with respect to a sonar of half-beamwidth 2.5 degrees and fish tilt angle distribution with parameters (0, 5) degrees for three gadoid species at two ultrasonic frequencies.

Species	Frequency (kHz)	$\hat{m}$	est[SE($\hat{m}$)]	$\hat{b}$	est[SE($\hat{b}$)]	SE	ρ	est[SE($\hat{b}_1$)]	ρ_2
Cod	38	20.8	0.9	−65.3	1.4	2.2	0.946	0.8	0.118
Cod	120	24.1	1.0	−72.3	1.5	2.2	0.963	1.4	0.515
Saithe	38	19.1	0.7	−62.4	1.0	1.4	0.967	0.6	−0.177
Saithe	120	18.9	0.8	−63.8	1.1	1.5	0.963	1.0	−0.208
Pollack	38	18.9	2.0	−63.6	2.9	1.6	0.824	1.7	−0.085
Pollack	120	15.3	2.8	−58.7	4.0	1.6	0.665	3.8	−0.267

cidences exist among the various regressions. This is done for the members of each set of regressions, which are distinguished by their common target strength type and manner of representation. The use of F-tests allows assignment of significance levels to the coincidences. These are considered both overall, or simultaneously with respect to both coefficients of the individual regressions under examination, and with respect to the slopes of the regressions.

The quantity of computation entailed by testing for coincidences among regressions based on the derived data can be reduced, which is evident by consideration of equations (1), (3), and (4) or equations (5) and (6). The equivalence of the three representation schemes for target strength data which are homogeneous in frequency establishes the equivalence of all comparisons of regressions of the same frequency-homogeneous data when expressed according to the three schemes. The identical frequency content of the corresponding regression coefficients in wavelength- and length-normalized representations, cf. equations (5) and (6), establishes the equivalence of corresponding tests for coincidences in the two normalized representation schemes. The labor of computation and presentation of results are thus simplified.

Results

The computed significance levels of various coincidences among the regressions are presented in Tables 5 and 6. The coincidences are considered for merging

TABLE 5. Levels of significance of overall coincidences among regressions of maximum or averaged dorsal aspect target strengths on fish length for three gadoid species at two ultrasonic frequencies.

Description of merged data		Target strength (TS) type					
		Maximum dorsal aspect TS		Averaged TS with parameters (−4.4, 16) degrees		Averaged TS with parameters (0, 5) degrees	
Species	Frequency (kHz)	Unnormalized representation	λ- or ℓ-normalized representation	Unnormalized representation	λ- or ℓ-normalized representation	Unnormalized representation	λ- or ℓ-normalized representation
Cod	38 and 120	0.239	$<10^{-7}$	$<10^{-7}$	$<10^{-7}$	$<10^{-6}$	$<10^{-7}$
Saithe	38 and 120	0.076	0.026	$<10^{-7}$	$<10^{-7}$	$<10^{-6}$	0.004
Pollack	38 and 120	$<10^{-4}$	0.446	$<10^{-3}$	0.417	0.386	0.362
Gadoids[a]	38	$<10^{-5}$	$<10^{-5}$	$<10^{-7}$	$<10^{-7}$	$<10^{-3}$	$<10^{-3}$
Gadoids	120	$<10^{-3}$	$<10^{-3}$	$<10^{-4}$	$<10^{-4}$	$<10^{-5}$	$<10^{-5}$
Gadoids	38 and 120	$<10^{-7}$	$<10^{-7}$	$<10^{-7}$	$<10^{-7}$	$<10^{-7}$	$<10^{-7}$

[a]All three gadoid species.

TABLE 6. Levels of significance of coincidences among slopes of regressions of maximum or averaged dorsal aspect target strengths on fish length for three gadoid species at two ultrasonic frequencies.

Description of merged data		Target strength (TS) type		
Species	Frequency (kHz)	Maximum dorsal aspect TS	Averaged TS with parameters (−4.4, 16) degrees	Averaged TS with parameters (0, 5) degrees
Cod	38 and 120	0.750	0.024	0.020
Saithe	38 and 120	0.050	0.450	0.831
Pollack	38 and 120	0.405	0.188	0.295
Gadoids	38	0.129	0.078	0.262
Gadoids	120	0.003	$<10^{-4}$	$<10^{-4}$
Gadoids	38 and 120	0.002	$<10^{-4}$	$<10^{-3}$

of derived target strength data of a given type with respect to frequency and species, both separately and together. Significance levels of overall coincidences among regressions are presented in Table 5. Significance levels of coincidences among slopes of regressions are presented in Table 6.

To illustrate the meaning of the significance levels of Tables 5 and 6, several significance levels of Table 5 are considered. The first number, 0.239, represents the probability of incorrectly rejecting the hypothesis that the maximum dorsal aspect target strength data for cod can be merged in frequency according to the unnormalized representations. This number would generally be too large to justify rejecting the hypothesis. The respective significance level for the representation of the same frequency-merged data according to the wavelength- and length-normalized representation schemes; namely, something less than 10^{-7}, would by most criteria justify rejecting the hypothesis of valid merging.

Discussion

The significance levels shown in Table 5 for overall coincidences among the target strength regressions are generally very low. In certain cases of species-homogeneous data the computed regressions appear coincidental, i.e. some species-segregated data appear to be homogeneous in frequency. No general advantage is associated with representation of the target strength data either with or without normalization. In the case of maximum dorsal aspect target strengths the cod data appear to be homogeneous with respect to frequency in the unnormalized representation, but not in the normalized representations, while the reverse is true for the pollack data. Homogeneity of the maximum dorsal aspect target strengths of saithe in frequency may be considered only marginally likely.

Application of the same confidence tests to the averaged target strengths yields somewhat similar results. For the averaged target strengths with averaging parameters (−4.4,16) degrees, only the frequency combination of normalized pollack data appears to be justified. The sole example of homogeneity among the averaged gadoid target strengths with averaging parameters (0,5) degrees appears to be that of frequency homogeneity among the pollack data, which obtains with or without normalization. The significance of apparent frequency homogeneity among these averaged pollack target strength data may be discounted in view of the smaller number of data and their rather limited length range compared to the cod and saithe data, cf. Table 1 and Fig. 1. Thus the general finding of significant frequency and species differences among the maximum dorsal aspect target strengths is enhanced with respect to the averaged target strengths. As averaged target strengths are of greater importance in the interpretation of acoustic estimates of fish abundance, establishment of target strength-to-fish length regressions for use in such interpretation ought to respect frequency and species differences in the backscattering of sound by fish.

Coincidences among slopes of target strength regressions occur more frequently than overall coincidences among the same regressions, which is evident from comparison of corresponding significance levels in Tables 5 and 6. This is not surprising when the basic length dependence of backscattering cross section is considered. For the ultrasonic frequencies and fish lengths of application this dependence is approximately quadratic. Deviations from a pure quadratic length dependence can, however, be significant. These depend, generally, on the frequency and species of application, although establishment of the length dependence of a target strength regression from inhomogeneous data may be justified in particular cases.

The fundamental question as to the legitimacy of merging target strength data which are inhomogeneous in species or frequency, which was raised at the outset of this study, is thus answered negatively in general. There may be justification for merging target strength data in some cases, especially with respect to the determination of the slope or length dependence of target strength regression, but this must depend on the particular data of application.

The precedent question on the manner of representing target strength data may now be answered. In so far as target strength data are intrinsically inhomo-

geneous in frequency or species they ought not to be merged, in which case choice of a representation scheme is immaterial as all are equivalent. As none of the three representation schemes considered here facilitates merging of frequency and species inhomogeneous data more than the others, use of the unnormalized representation may be considered superior to use of either of the two normalized representations. The reason is twofold: Occam's razor demands simplicity and the unnormalized scheme is free from the arbitrary, physically unjustified frequency factor present in the normalized representations, cf. equations (5b) and (6b), except in the case of a pure quadratic length dependence of backscattering cross section when the frequency factor vanishes.

The use of either normalized representation scheme does facilitate merging of some target strength data that are widely disparate in length and frequency. The legitimacy of such merging must be suspect, however, because of its reliance on the scaling hypothesis. For the data of this study, the scaling hypothesis has been refuted by the demonstration that target strength data that are homogeneous in species cannot generally be combined in frequency according to either of the normalized representation schemes.

The practical consequence of this study to fisheries research, e.g. in the acoustic surveying of definite fish stocks, may be summarized thus: Derivation of target strength-to-length regressions for use in the interpretation of acoustic measurements should respect both the fish species of observation and the ensonification frequency.

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Relationships Between RNA–DNA Ratio, Prey Density, and Growth Rate in Atlantic Cod (*Gadus morhua*) Larvae

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BUCKLEY, L. J. 1979. Relationships between RNA–DNA ratio, prey density, and growth rate in Atlantic cod (*Gadus morhua*) larvae. J. Fish. Res. Board Can. 36: 1497–1502.

The protein, DNA, and RNA content of larvae maintained at 1.0 plankter/mL increased at the rates of 9.3, 9.9, and 9.8% per day, respectively, for the 5 wk after hatching. Protein reserves of larvae held at 0 or 0.2 plankters/mL were depleted by 45 and 35%, respectively, prior to death 12–13 d after hatching. Starved larvae had similar protein concentrations (percent of dry weight), lower RNA concentrations, and higher DNA concentrations than fed larvae. Larvae held at higher plankton densities had higher RNA–DNA ratios and faster growth rates than larvae held at lower plankton densities. The RNA–DNA ratio was significantly correlated ($P < 0.01$) with the protein growth rate. The RNA–DNA ratio appears to be a useful index of nutritional status in larval Atlantic cod (*Gadus morhua*) and may be useful for determining if cod larvae were in a period of rapid or slow growth at the time of capture.

Key words: RNA–DNA ratio, starvation, protein, nucleic acids, growth, larval fish, Atlantic cod

BUCKLEY, L. J. 1979. Relationships between RNA–DNA ratio, prey density, and growth rate in Atlantic cod (*Gadus morhua*) larvae. J. Fish. Res. Board Can. 36: 1497–1502.

La teneur en protéines, en ADN et en ARN de larves maintenues dans un milieu contenant 1,0 planctonte/mL a augmenté respectivement de 9,3, 9,9 et 9,8% par jour pendant les cinq semaines qui ont suivi l'éclosion. Les réserves protéiques des larves maintenues dans un milieu contenant 0 ou 0,2 planctonte/mL ont baissé respectivement de 45 et de 35% avant la mort, survenue 12 à 13 jours après l'éclosion. Les larves affamées présentaient une teneur similaire en protéines (pourcentage du poids sec), moindre en ARN et plus forte en ADN que les larves nourries. Les larves maintenues dans un milieu à forte densité de plancton présentaient des rapports ARN/ADN et des taux de croissance plus élevés que les larves se trouvant dans un milieu pauvre en plancton. Le rapport ARN/ADN présentait une corrélation significative ($P < 0,01$) avec le taux d'augmentation des protéines. Ce rapport semble un indice utile de la nutrition des larves de morue (*Gadus morhua*) et peut servir à déterminer si elles sont dans une période de croissance lente ou rapide au moment de la capture.

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THE mechanisms that maintain fish stocks at their observed levels are thought to operate primarily during the early life stages, particularly the larval stage when mortality due to starvation and predation is usually the greatest and most variable (Hunter 1976). Presently, there is no single, generally accepted and widely used technique for the diagnosis of the starving condition in larval fish, although a multivariate approach combining several morphometric measurements or histological criteria may be useful (Theilacker 1978). Assessments of larval condition based on length–weight relationships and morphometrics suffer from problems related to preservation, allometric growth, ossification, and simultaneous loss of length and weight (Blaxter 1971). Establishment of criteria for the evaluation of larval condition or viability are considered essential for an understanding of the role of starvation in the stock-recruitment relationship.

The ratio of ribonucleic acid (RNA) to deoxyribonucleic acid (DNA) has been related to both long-term and recent growth in adult freshwater fish. Haines (1973) demonstrated a significant positive correlation between population growth over a 15-mo period and the RNA–DNA ratio of muscle tissue from smallmouth bass (*Micropterus dolomieui*) and carp (*Cyprinus carpio*). Bulow (1970, 1971) reported that RNA–DNA ratios were very sensitive to changes in feeding levels and could be used as an indicator of recent growth rates in adult golden shiners (*Notemigonus crysoleucas*). Buckley (1979a, b) found that the RNA–DNA ratio was useful for the diagnosis of the starving

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condition in winter flounder (*Pseudopleuronectes americanus*) larvae.

The present study was initiated to determine the changes in total DNA, RNA, and protein content during development of Atlantic cod (*Gadus morhua*) larvae at different prey densities in order to define the effects of starvation and the relationships between the RNA–DNA ratio, prey density, and growth rate.

Materials and Methods

Adult Atlantic cod were captured by trawl net off Rhode Island, USA, and kept in a 28 000-L tank. The fish were induced to spawn by manipulating photoperiod and water temperature. Fertilized eggs were collected daily with a 0.5-m plankton net. The eggs were incubated, and the larvae were reared in 64-L aquaria at 7°C. Larvae were fed live zooplankton collected in the Narragansett Bay area after sieving to select the appropriate size fraction. The diet consisted mainly of rotifers and copepod nauplii and copepodites. For experiments in which larvae were kept at a constant prey density, about 1000 larvae were transferred 4 d after hatching to 38-L aquaria. The concentration of zooplankton was adjusted daily to 0.2 or 1.0 plankters/mL. Larvae maintained at a fluctuating plankton density (FPD) were fed at concentrations exceeding 4 plankters/mL when available and allowed to drop to less than 0.2 plankters/mL at other times.

Nine populations of laboratory reared larvae were studied. Samples for chemical analysis and dry weight determination were taken from each population at 2–3-d intervals from hatching to day 11 and thereafter at 6–8-d intervals until the experiments were terminated at about week five. Because of the susceptibility of nucleic acids to enzymatic and heat degradation, homogenization and extraction were carried out on fresh material at temperatures between 0 and 4°C. This protocol precluded obtaining dry weights on the same larvae used for nucleic acid analysis. Triplicate samples consisting of between 2 and 30 larvae each were homogenized immediately after sampling in 2 mL of ice-cold reagent grade water with a motor driven all glass tissue grinder. The number of larvae per sample was chosen to give between 250 and 1000 μg of protein. Duplicate 0.1-mL samples of homogenate were frozen for later protein analysis using a modification of the Lowry method (Hartree 1972). Bovine serum albumin (BSA) was used as standard. Nucleic acids were extracted and partially purified from 1.4 mL of homogenate using a modification of the Schmidt–Thannhauser method (Munro and Fleck 1966) as outlined in Fig. 1. RNA and DNA were estimated from the absorbancy at 260 nm of the appropriate hydrolysate.

Dry weights were obtained on separate samples of 10 larvae each. Larvae were rinsed in distilled water, freeze-dried, and weighed to the nearest microgram on an electrobalance. After weighing, the larvae were homogenized in 1 mL of water and analyzed for protein as described above.

Up to day 17 the coefficient of variability (sample standard deviation as percent of the mean) of the triplicate analyses was 6% for protein, 7% for DNA, 6% for RNA, and 6% for the RNA–DNA ratio. After day 17 the coefficient of variability increased for all analyses, giving overall values of 9% for protein, 11% for DNA, 10% for RNA, and 8% for the RNA–DNA ratio. The larger variability in the data for older larvae was probably due in large part

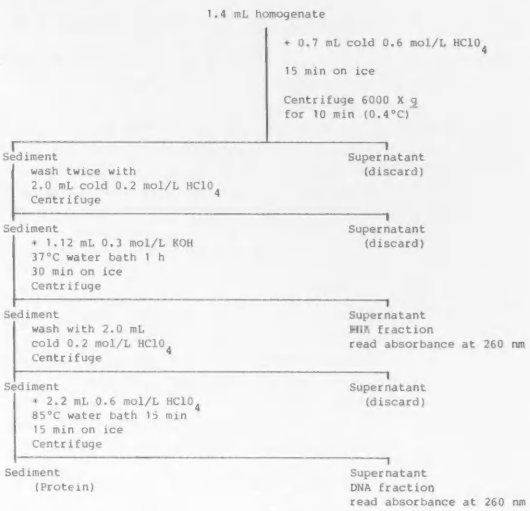

FIG. 1. Procedure for estimating RNA and DNA in larval fish.

to the large size range of individuals of the same age and the smaller number of individuals sampled.

The protein growth coefficient (Gp) expressed as the percent change in protein content per day was calculated from the slopes of the regression equations describing the relationship between the natural logarithm of the protein content (μg/larvae) as the dependent variable and the age in days as the independent variable. RNA and DNA growth coefficients were calculated in the same way. The daily specific protein growth rate (SGRp) for an interval was calculated from the formula:

$$\mathrm{SGR}p = [10^{(\log W_{n+t} - \log W_n)/t} - 1]\cdot 100$$

where W_n is the protein content at time n and t is the interval in days.

Results

Larvae held at 1 plankter/mL began feeding 4–6 d after hatching. The protein and RNA content of larvae in this group increased steadily from day 7 to day 38 (Fig. 2). The RNA content of larvae held at a fluctuating plankton density showed two periods of decline during the same period. The DNA content of larvae held at both higher plankton densities fluctuated until day 17, after which a steady increase was observed. The protein, DNA and RNA growth coefficients were 9.3, 9.9, and 9.8% per day at 1 plankter/mL. The protein growth coefficient was 6.4% per day at FPD.

Larvae held at 0.2 plankters/mL responded similarly to starved larvae, the majority dying 12–13 d after hatching. A few larvae held at 0.2 plankters/mL survived to day 15 when the tank was broken-down. The patterns of change in RNA, DNA, protein and the RNA–DNA ratio observed at 0 and 0.2 plankters/mL (Fig. 2 and Table 1) were very similar and clearly

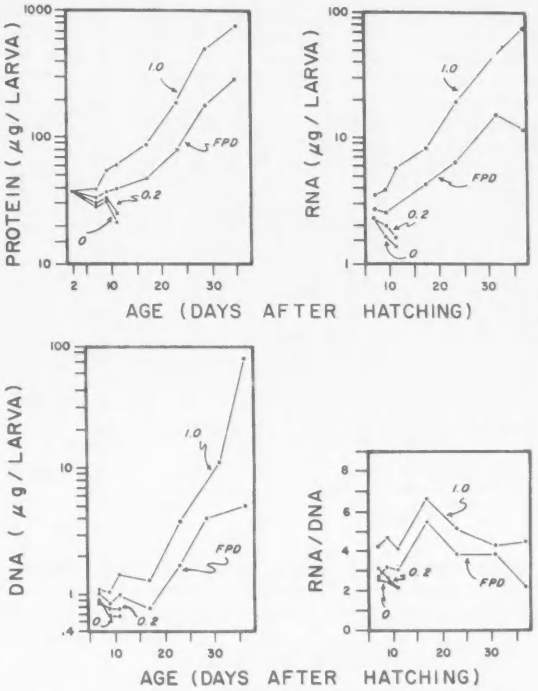

FIG. 2. Changes in the RNA–DNA ratio, protein, RNA, and DNA content of larval cod during development at four prey densities. Data points are means of three replicate samples containing 12–30 larvae each. The four prey densities used were 0, 0.2, and 1.0 plankters/mL and a fluctuating plankton density (FPD) ranging from less than 0.2 to greater than 4 plankters/mL.

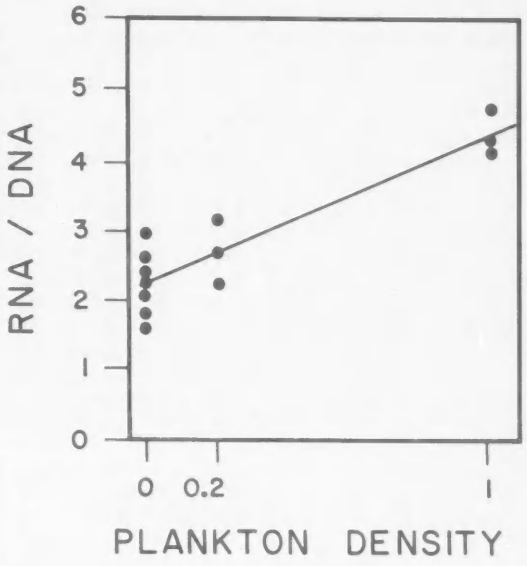

FIG. 3. Relationship between zooplankton prey density and the RNA–DNA ration of cod larvae 7–11 d after hatching. Points represent data for pooled samples of 12–20 larvae each.

showed the effects of starvation. Net decreases in protein and nucleic acid content as well as the RNA–DNA ratio were observed between 7–11 d after hatching at both lower prey densities. By day 11, the unfed larvae had lost 45% of their protein present on day 2, and larvae held at 0.2 plankters/mL had lost 35%.

The protein concentration (% dry weight) of larvae in all four groups were very similar on each sampling day, all decreasing between day 2 and day 11 (Table 1). No relationship between feeding level and protein concentration was apparent. However, the RNA concentration was higher and the DNA concentration lower in larvae held at 1 plankter/mL than in starved larvae.

A direct linear relation ($P < 0.01$) between the RNA–DNA ratio and prey density was observed for cod larvae 7–11 d after hatching (Fig. 3). The relation was not tested prior to day 7 because the larvae had not established feeding; or after day 11 because of the large mortalities at the two lower plankton densities.

The relation between the RNA–DNA ratio and the percent change in protein content per day was examined for a wide range of time intervals and growth rates. Over the entire period studied, less than 2 wk for starved larvae and 6 wk for fed larvae, a direct linear relation ($P < 0.01$) was observed between the protein growth exponent of a population and the mean of the subweekly RNA–DNA ratio estimates (Fig. 4). Similar linear relations were observed for individual RNA–DNA ratio estimates and the change in protein content over intervals up to 8 d before or after the nucleic acid measurement (Table 2). The relation was not significant ($P > 0.05$) for intervals longer than 8 d and could not be tested for intervals shorter than two days because of the limitations of the method for estimating the change in protein content. The mean of two consecutive RNA–DNA ratio estimates was linearly related ($P < 0.01$) to the percent change in protein content over the interval between the nucleic acid measurements.

Discussion

The minimum prey density required for growth and survival of cod larvae under our experimental conditions apparently lies between the 0.2 and 1.0 plankter/mL. Larvae maintained at 0.2 plankters/mL responded similarly to starved larvae, rapidly depleting their protein and RNA reserves. Protein catabolism from the start of starvation has also been observed in larval plaice (*Pleuronectes platessa*) (Ehrlich 1974a), larval herring (*Clupea harengus*) (Ehrlich 1974b), and larval winter flounder (Buckley 1979b). Even in the presence of an apparent excess of food organisms, we have observed

TABLE 1. Dry weight, protein, DNA, and RNA concentration of Atlantic cod larvae under four feeding regimes. Protein, RNA, and DNA data are means of three replicate samples containing 12–30 larvae each. Dry weight data are means of 10 larvae.

Age (d)	Plankton density (plankters/mL)	Dry weight (μg)	Protein (% dry weight)	RNA (% dry weight)	DNA (% dry weight)
2		51	76		
7	1.0	65	61	7.1	1.7
	FPD[a]	62	54	4.4	1.6
	0.2	59	51	4.6	1.5
	0	48	58	4.8	1.8
9	1.0	102	54	4.8	1.0
	FPD	68	55	3.7	1.2
	0.2	64	52	3.2	1.2
	0	53	61	3.1	1.3
11	1.0	134	45	4.3	1.1
	FPD	80	49	3.7	1.2
	0.2	56	45	2.9	1.4
	0	44	48	3.1	1.6

[a]Fluctuating plankton density.

net protein catabolism in cod and winter flounder larvae for the first 7–9 d after hatching. These observations and the low carbohydrate content of larval marine fish (Ehrlich 1974b) suggest that protein is an important energy source during the period immediately after hatching, although in some species lipid catabolism is quantitatively more important (May 1971).

Although the data presented in Fig. 2 indicate net protein synthesis between day 2 and day 11 in larvae held at 1.0 plankters/mL and net protein catabolism in larvae held at 0 and 0.2 plankters/mL, their protein concentrations (% dry weight) were very similar through the period (Table 1). May (1971) reported that unfed California grunion (*Leuresthes tenuis*) larvae had lower fat and the same or slightly higher protein concentrations than fed larvae. Apparently, starvation induced changes in protein content are accompanied by corresponding changes in other components, principally lipids, resulting in little change in protein concentration.

The dry weight of larval marine fish is the sum of the weights of a large number of organic and inorganic constituents of which protein and fat are generally quantitatively the most important. A change in the content of any single constituent can result in a change in the concentration of all the other constituents. Also, a change in one component can be masked by a change in one of the more abundant components when the data is expressed in terms of percent. For these reasons expressing data on chemical composition in terms of content (micrograms per larvae) rather than concentration (% dry weight) may be more informative and more accurately reflect the changes that take place during starvation. Comparisons between larvae of different sizes are best made using the relationship between length

TABLE 2. Relations between the percent change in protein content per day (SGRp) and the RNA–DNA ratio for the period from feeding initiation to 42 d after hatching. The daily specific protein growth rate (SGRp) was calculated for the intervals:

$$n - t_1,\ n,\ n + t_2$$

using the formula:

$$\mathrm{SGR}p = [10^{(\log W_{n+t} - \log W_n)/t} - 1] \cdot 100$$

where W_n is the protein content of a larvae at time n and t is an interval ranging from 2 to 8 d.

	X	(SGRp)	Slope	Intercept	n	r
1	$(\mathrm{RNA/DNA})_n$	$n - t_1$ to $n + t_2$	3.84	−10.49	22	0.84[a]
2	$\dfrac{(\mathrm{RNA/DNA})_{n-t} + (\mathrm{RNA/DNA})_n}{2}$	$n - t_1$ to n	4.91	−13.83	20	0.88[a]
3	$(\mathrm{RNA/DNA})_n$	$n - t_1$ to n	3.91	−11.64	25	0.74[a]
4	$(\mathrm{RNA/DNA})_n$	n to $n + t$	4.98	−15.36	22	0.77[a]

[a]$P < 0.01$.

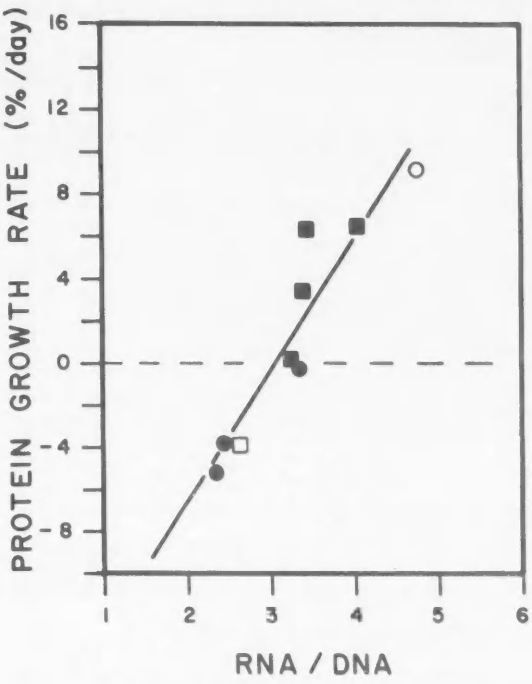

FIG. 4. Relationship between the mean RNA–DNA ratio and the protein growth rate of nine laboratory populations of cod larvae. ○ . . . 1 plankter/mL; ■ . . . fluctuating plankton density □ . . . 0.2 plankter/mL; ● . . . 0 plankter/mL.

and body constituents similar to those reported for dry weight, RNA, DNA, and protein in cod and winter flounder larvae (Buckley 1979a).

The magnitude of the decrease in the total RNA content of starved cod larvae, exceeding 50% in 4 d, cannot be accounted for entirely by a net breakdown of messenger RNA which makes up only a small percentage of the total RNA. Other types of RNA including ribosomal RNA must also be involved. Because DNA was largely conserved through the period of starvation a decrease in the RNA–DNA ratio was observed. Similar decreases in the RNA–DNA ratio of starved winter flounder larvae (Buckley 1979b) and adult golden shiners (Bulow 1970) have been reported. Starvation of adult rats led to large reductions in the total liver ribosomal and nonribosomal RNA, while total liver DNA was unaffected (Hayashi and Kaymievowski 1972). Blobel and Potter (1976) reported that the RNA–DNA ratio of livers from starved rats increased within 12 h of refeeding. Recovery to control values required several days (Stocco et al. 1976).

In the laboratory at constant temperature, feeding success and growth of larval marine fish are largely controlled by prey density below saturation levels, i.e. until the prey numbers are greater than needed. The RNA–DNA ratio of larvae reflects both their past feeding success, as indicated by the relation between the RNA–DNA ratio and prey density shown in Fig. 3, and their past growth rate as indicated by Table 2. The RNA–DNA ratio is also an indicator of the potential future growth rate of a population (Table 2). Larvae with a high RNA–DNA ratio would be expected to grow (accumulate protein) at a faster rate than larvae with a low RNA–DNA ratio. However, larvae would only be expected to maintain a high RNA–DNA ratio and continue to grow at a fast rate if sufficient food was available. Although the RNA–DNA ratio reflects, and is at least partially determined by, past feeding success, it is not certain whether the effect of prey density on growth rate is actually mediated or simply accompanied by a change in the RNA–DNA ratio.

Because RNA serves as both a template and organizer for protein synthesis, the loss of RNA results in a decrease in the potential maximum rate of protein synthesis and may consequently limit growth. In fact, it has been postulated that control over the rate of protein synthesis is exerted by the rate of messenger RNA synthesis and breakdown. The RNA content of a wide variety of organisms has been related to growth rate (Sutcliffe 1970). The best correlations between RNA concentration and growth rate have been observed for organisms in a phase of exponential growth (Dagg and Littlepage 1972). The RNA–DNA ratio can be considered a measure of the amount of protein synthetic machinery per cell, since the DNA content of an organism is an indicator of cell number. Therefore, the direct positive relationships between RNA–DNA ratio and growth rate observed in this study were expected. Positive correlations between RNA–DNA ratio and growth rate have also been observed for adult golden shiners (Bulow 1970), smallmouth bass and carp (Haines 1973).

The RNA–DNA ratio appears to be a sensitive and reliable index of the nutritional state of cod and winter flounder larvae (Buckley 1979a, b), since the ratio falls within fairly well defined limits in fed larvae and is lower in starved larvae. The RNA–DNA ratio of cod larvae maintained at 1.0 plankter/mL ranged from 4.0 to 6.6. This is similar to the 3.5–6.0 range observed for fed winter flounder larvae (Buckley 1979a, b) and the 3.1–5.7 range reported for golden shiners fed at 6% of body weight per day (Bulow 1970). The RNA–DNA ratio of cod larvae maintained at 0 and 0.2 plankters/mL fell within the ranges of 2.0–2.6 and 2.2–3.2, respectively. This is similar to the 2.2–3.2 range observed for starved winter flounder larvae (Buckley 1979b). These findings suggest a relationship between the RNA–DNA ratio and nutritional condition in fish.

The general positive relationships between RNA–DNA ratio and protein growth rate of cod larvae observed in this study suggest that a single RNA–DNA measurement may be sufficient to determine if the larvae were experiencing a period of rapid or slow growth at the time of capture. Extension of this finding to other

species of larval fish should be made with caution since less extensive work with winter flounder larvae showed no significant correlation between RNA–DNA ratio and growth rate (L. J. Buckley unpublished data). The use of RNA–DNA ratios to reflect or predict growth rates and the relationships between RNA–DNA ratio and feeding success should be investigated further.

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Mode of Life and Feeding in Maldanid Polychaetes from St. Margaret's Bay, Nova Scotia

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HUGHES, T. G. 1979. Mode of life and feeding in maldanid polychaetes from St. Margaret's Bay, Nova Scotia. J. Fish. Res. Board Can. 36: 1503–1507.

The habits and behavior of *Axiothella catenata*, *Praxillella gracilis*, and *Nicomache lumbricalis* (Polychaeta: Maldanidae) are described. Each feeds from a different level in the sediment thereby reducing competition for food and space. All three maldanids are generally unselective in the material they ingest and from which they construct tubes. Thus within certain limits the particle size of the sediment is thought not to be a critical factor in determining their distribution and abundance. *Axiothella catenata* does not produce fecal pellets but particles are still aggregated in the gut and a large proportion of bacteria attached to sediment particles pass through the gut undigested. *Axiothella catenata* egests material in proportion to its size; a specimen of 4-mm internal tube diameter egests 1.10 ± 0.15 mL/d.

Key words: benthos, detritus feeders, Annelida, Polychaeta, Maldanidae

HUGHES, T. G. 1979. Mode of life and feeding in maldanid polychaetes from St. Margaret's Bay, Nova Scotia. J. Fish. Res. Board Can. 36: 1503–1507.

L'auteur décrit les habitudes et le comportement des espèces *Axiothella catenata*, *Praxillella gracilis* et *Nicomache lumbricalis* (polychètes de la famille des maldanidés). Chacune se nourrit dans les sédiments, à une profondeur différente, ce qui réduit la compétition pour la nourriture et l'espace. Les trois ne manifestent généralement pas de préférence dans le choix des matériaux qu'elles ingèrent pour construire leurs tubes. Toutes proportions gardées, la granulométrie des sédiments n'apparaît donc pas comme un facteur limitant de leur répartition et de leur abondance. Bien qu'*A. catenata* ne produise pas de boulettes fécales, des particules sont néanmoins agglutinées dans son intestin et un bon nombre des bactéries qui s'y trouvent sont éliminées sans avoir été digérées. L'espèce évacue des matières proportionnellement à sa taille; un spécimen dont le tube a un diamètre interne de 4 mm évacue 1,10 ± 1,15 mL/jour.

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POLYCHAETES of the family Maldanidae are often one of the major components of benthic populations (Newell 1951; Rhoads and Stanley 1965) and yet little is known of the general biology of most species. The genus *Clymenella*, a largely shallow water form, is well known because of the investigations by Pilgrim (1965), Mangum (1964a, b), Rhoads and Stanley (1965), Gage (1968), and others. However, species like *Axiothella catenata* (Malmgren), *Praxillella gracilis* (Sars), and *Nicomache lumbricalis* (Fabricius), found in large numbers in St. Margaret's Bay, Nova Scotia (Hughes 1979), are known only from work on their taxonomy and morphology (Arwidsson 1911, 1922; Nolte 1913; Wesenburg-Lund 1948).

This paper reports on some aspects of the biology of these species, especially their feeding mechanisms and relationship with the sediment they inhabit. Within the sediment sources of food may be debris particles, debris attached to mineral particles and bacteria attached to both the mineral and debris particles (Hughes 1979). The effect of ingestion on each of these components was examined together with observations on the selection of particles for ingestion and the rate at which food is passed through the gut.

Materials and Methods

Material was obtained from the region of St. Margaret's Bay studied earlier (Hughes 1979) by means of a van Veen grab. Orientation of the animals and their tubes was observed by placing the sediment sample, still contained in the grab, in a deep freeze. Later the sediment was slowly washed away to reveal the animals in situ. Habits and behavior were observed by introducing specimens into glass tanks containing sediment from the sampling area, in running seawater cooled to the natural temperature (2–5°C).

Gut contents of *A. catenata*, *P. gracilis*, and *N. lumbricalis* were examined and measured to determine if food particles were selected by size. Four specimens of each species were

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allowed to burrow in natural sediment and, after feeding had continued for several days, were removed and any ingested sediment was extracted from the foregut. The size of mineral particles ingested, and of those sampled from the surrounding sediment and the tubes of the specimens was measured directly under the microscope: they ranged in size from 90 to 150 μm. Only the mineral component of these samples was measured as debris particles usually became stuck together in the mucus secreted by the animal.

The effect of ingestion on the relative amount of debris adsorbed onto mineral particles was examined using four specimens of *A. catenata* (internal tube diameter 4.0–4.65 mm) established in sediment of size range 75–500 μm at 4.0°C. After 10 d, samples of sediment were taken from the feeding area and from the portion of the gut within the last seven segments of the body (Pilgrim 1965). A microscope fitted with a camera lucida was used to trace the outlines of 50 randomly selected mineral particles and their adsorbed debris from each sample. The percentage area of each particle covered by debris was then determined by planimetry. Results were expressed as the frequency with which different levels of coverage occurred in the samples. This method, however, only allowed the debris on one surface of a particle to be estimated and it was assumed that this was a function of the debris on the whole particle.

Examination of the effects of ingestion on bacteria attached to sediment particles and on the size of debris particles was made by maintaining three specimens of *A. catenata* in natural sediment for 10 d until all were feeding well. Samples of sediment were then removed from the feeding area, the fecal pile, and the posterior intestine of each specimen. Using the methods of the earlier study (Hughes 1979) these samples were stained with acridine orange and examined by fluorescent microscopy for bacteria attached to the particles. In addition the size distribution of debris particles from the feeding area and the posterior intestine was determined by direct measurement.

To estimate the egestion rate of *A. catenata* 12 specimens were kept in individual trays of natural sediment at 1.5–2.5°C. After 7 d all the specimens were feeding and the fecal piles were cleared away so that measurements could begin. At 24-h intervals the fecal material produced by each specimen was collected, dried overnight at 60°C, and weighed. After 14 d the animals were removed and the most reliable estimate of their size, the internal diameter of their tubes, was measured. Dry weight of the sediment egested was converted into volume by estimating the weight of a given volume of the sediment.

Results

Habits and Behavior

Axiothella catenata occurred in St. Margaret's Bay with an abundance of 38–65/m^2 and lived in a straight or gently curved tube composed of sediment particles glued together; the larger tubes had an internal diameter of about 8 mm and lengths of at least 40 cm. One end was positioned at the surface, and the tube sloped gently into the sediment so that the other end was up to 15 cm deep (Fig. 1a). Branches were often built from the tube, permitting the animal to shift its feeding position; once a new branch was in use any old ones quickly disintegrated. Animals without tubes, allowed to burrow in sediment, quickly formed new ones by secreting from the anterior end a covering of mucus to which a layer of sediment adhered. The animal then moved forward to form another portion of the tube and after three or four movements the whole of the body was enclosed. When first formed the tube was soft but hardened after several days.

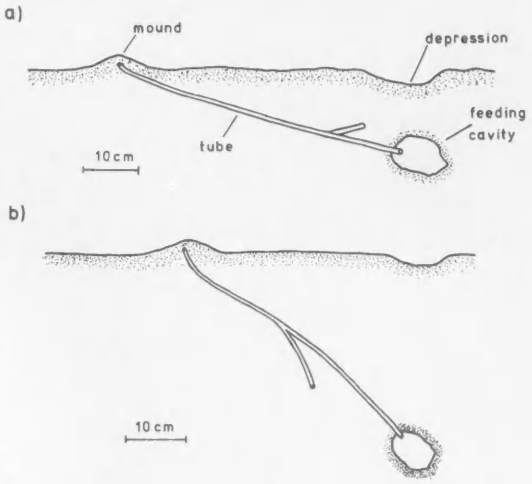

FIG. 1. Positions of the tubes of a) *Axiothella catenata* and b) *Praxillella gracilis* in the sediment.

All the specimens of *A. catenata* examined had their tails nearest the surface of the sediment and their heads at depth. The animal ingested sediment, using its

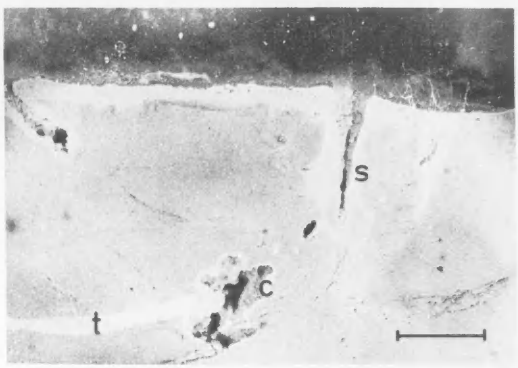

FIG. 2. Photograph of a tube (t) of *A. catenata* constructed against the glass of an aquarium showing the cavity (c) and the subsidence (s) caused by feeding activity (bar = 5 cm).

bulbous proboscis, from the subsurface end of the tube to form a sizeable feeding cavity (Fig. 2). Water was circulated through this cavity by undulations of the body wall, causing the sediment of the walls to become oxidized and thus lighter in color than the surrounding sediment. Very often the roof of the feeding cavity collapsed, bringing fresh sediment to the animal and leaving a depression at the surface. A little distance from this depression was a mound of fecal material deposited around the surface end of the tube (Fig. 1a). The animal periodically moved up to the surface from its feeding position near the bottom of the tube to defecate.

Praxillella gracilis was found in the same region as *A. catenata* but was less numerous (18–33/m²). Its tube was similar to that of *A. catenata* but had thinner walls and tended to be more brittle; branches were numerous. The tube lay at a fairly steep angle in the sediment so that, although this species was generally smaller, its tube penetrated up to 30 cm into the sediment (Fig. 1b). A feeding cavity was also formed at the subsurface end of the tube and, again, caused depressions on the surface. Feces, in the form of loose strings, were deposited around the surface or tail end of the tube.

Nicomache lumbricalis was found with *A. catenata* and *P. gracilis* in densities of 5–13/m² but was much more abundant in shallower water. The tube was also composed of sediment particles but was much coiled, usually together with other tubes, to form a globular colony. The colony lay free in the sediment or was attached to a stone or fragment of shell but was never very far beneath the sediment surface. *N. lumbricalis* also feeds entirely on sediment particles but appears to be much less mobile than *A. catenata* or *P. gracilis*.

Selection of Particles for Ingestion

None of the samples of mineral particles from the gut of *A. catenata* was significantly different in size distribution from those of the sediment (Kolmogorov-Smirnov test, two tailed, $P = 0.05$). The tubes, except for that of one specimen, were also composed of particles similar to those of the sediment. *Praxillella gracilis*, too, showed no difference between the size distribution of its gut contents, tube and the sediment it fed upon. However, material ingested by one specimen of *N. lumbricalis* differed from its sediment, as did particles from two of the tubes. Generally there were few differences between gut contents and the sediment, suggesting that active selection of particles for ingestion in these species is unlikely. *Nicomache lumbricalis* generally inhabited and fed upon a coarser sediment than that ingested by *P. gracilis* (Table 1). The material it ingested and from which it made its tube was also coarser than that used by *P. gracilis*. *Axiothella catenata* lived in the same sediment as *P. gracilis* so that the material it ingested was also different to that of *N. lumbricalis*.

Table 1. Comparison of the size distribution of mineral particles in the natural sediment (Sed), the gut (G), and tubes (T) of *N. lumbricalis* and *P. gracilis* (Kolmogorov-Smirnov test, one tailed, $P = 0.05$). The numbers 1, 2, 3, and 4 are the specimen numbers; 1G therefore refers to particles from the gut of specimen 1.

Comparison				
Nicomache		Praxillella	Result	Indication
Sed	–	Sed	$<.001$	(Nic > Prax)
1G	–	1G	$<.01 > .001$	(Nic > Prax)
2G	–	2G	$<.01 > .001$	(Nic > Prax)
3G	–	3G	$<.1 > .05$	(Nic = Prax)
4G	–	4G	$<.001$	(Nic > Prax)
1T	–	1T	$<.001$	(Nic > Prax)
2T	–	2T	$<.001$	(Nic > Prax)
3T		3T	$<.001$	(Nic > Prax)
4T		4T	$<.001$	(Nic > Prax)

A. catenata — Effect of Ingestion on the Size Adsorbed onto Mineral Particles

The four sediment samples used were statistically similar to each other in their amounts of adsorbed debris (Mann-Whitney U-test, two tailed, $P = 0.05$). Similarly, samples from the posterior intestine of the four specimens of *A. catenata* were comparable but each had a greater amount of debris than the corresponding sediment sample (Mann-Whitney U-test, one tailed, $P = 0.05$) (Fig. 3). Compared with the sediment, the intestine contained fewer mineral particles with small amounts of debris and a greater number with larger amounts of debris.

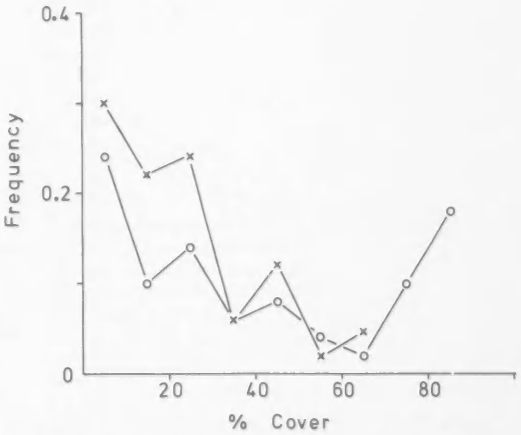

Fig. 3. The relative amount of debris attached to mineral particles from the sediment (×) and the posterior intestine (○) of a specimen of *A. catenata*.

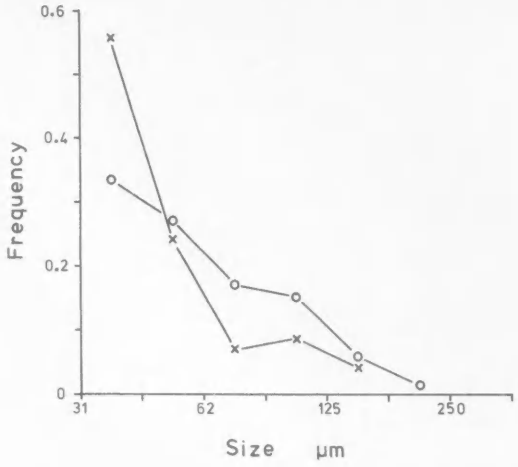

FIG. 4. Size distribution of debris particles in the sediment (×) and from the posterior intestine of a specimen of *A. catenata* (○).

A. catenata — EFFECT OF INGESTION OF THE SIZE DISTRIBUTION OF DEBRIS PARTICLES

In all three specimens debris from the posterior intestine was coarser than the debris in the sediment fed to the animals (Kolmogorov-Smirnov test, one tailed, $P = 0.05$) (Fig. 4). No differences were found between the size distribution of debris in the sediment samples or between those of the specimens (Kolmogorov-Smirnov test, two tailed, $P = 0.05$).

A. catenata — EFFECT OF INGESTION ON BACTERIA ASSOCIATED WITH SEDIMENT PARTICLES

Qualitative observations on the bacteria of the sediment samples indicated that their distribution and abundance was similar to that described in an earlier paper (Hughes 1979), the cells being found on all particles except small mineral flakes. Particles from the posterior intestine of *A. catenata* still had bacteria on them. Large mineral and debris particles still had intact bacterial cells spread over their surfaces, and diatom remains and other recognizable fragments still supported the highest numbers of bacteria, as was found in the sediment samples. Only small debris particles appeared to have bacterial populations reduced as a result of ingestion. Particles from the fecal mound also supported levels of bacteria comparable to the sediment, but these may have been recolonized after defecation.

A. catenata — EGESTION RATES

From the first to the eighth day of the experiment all 12 specimens consistently increased the amount of sediment they egested. Whilst some of the specimens stabilized after day 8, only at day 11 were all egesting relatively constant amounts. Thus, only the amounts egested over the last 4 d of the experiment were averaged for each specimen and plotted against the size of the animal, measured as the internal diameter of the tube (Fig. 5). A double-log transformation gave the best fit and produced the regression equation, $\log_{10} Y = 1.265 \log_{10} X - 0.7199$.

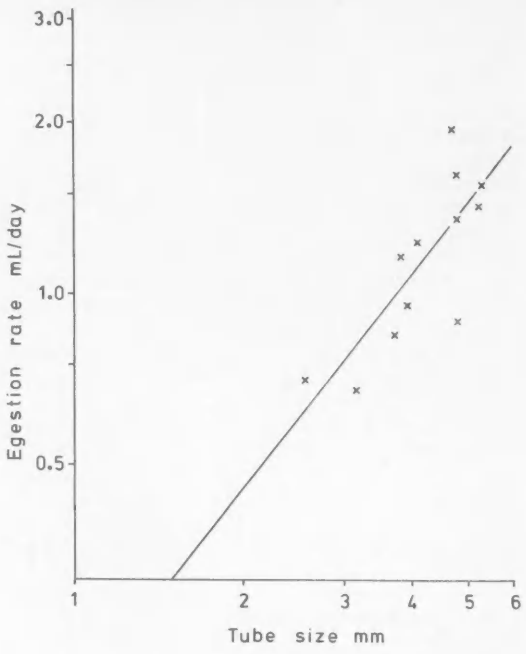

FIG. 5. Relationship between the size of *A. catenata* (internal diameter of tube) and its egestion rate.

Discussion

The habits of *A. catenata* and *P. gracilis* are, in general, similar to those of *Clymenella torquata* (Rhoads and Stanley 1965; Gage 1968) but, whereas the latter has a vertical tube, *A. catenata* and *P. gracilis* both have sloping ones. Although *A. catenata* is generally larger, the shallow angle of its tube means it is feeding at a depth of about 15 cm compared with 30 cm for *P. gracilis*. *Nicomache lumbricalis*, however, feeds from near the surface of the sediment. The vertical distribution of these species, which all occur together and with other deposit feeding organisms, probably acts to reduce competition for food and space (Mangum 1964a).

Maldanids have a very simple feeding proboscis which, as indicated by the present investigation, is probably incapable of selecting between individual particles. Thus, the greater amounts of adsorbed debris on mineral grains from the gut of *A. catenata* more likely result from debris being stuck onto them during their passage through the gut than from any active selection of heavily coated mineral grains during ingestion. In contrast, the bivalve mollusk *Abra tenuis* can select for ingestion mineral grains with a high load of adsorbed

debris (Hughes 1977), but this species has complex feeding appendages capable of selecting between individual particles. Similarly, debris particles also increase in size within the gut even though *A. catenata* does not form fecal pellets like *Yoldia* (Rhoads 1963) and *Nucula* (Young 1971), a process that necessarily aggregates particles. Thus, although these animals are probably reducing organic debris by digestion (Poulet 1976; Tenore 1976) they also appear to be aggregating debris and other particles.

Bacteria from cultures are reported to be utilized with high efficiency by marine invertebrates (Fenchel 1970; Hargrave 1970; Wavre and Brinkhurst 1971; Kofoed 1975a, b) but whether this holds for natural populations of bacteria attached to sediment particles may be questioned. Certainly material in the intestine of *A. catenata* and *Arbarenicola* (Hylleberg 1975) has substantial numbers of bacteria still attached, suggesting a relatively low utilization. Whatever the reasons for this discrepancy, they will not be discovered by direct observation and counting until techniques are greatly improved.

A moderately sized specimen of *A. catenata* (4 mm internal tube diameter) is estimated to egest 1.10 ± 0.15 mL/d of sediment. By comparison the egestion rate of *Clymenella* is estimated to range from 0.75 mL/d (Rhoads and Stanley 1965) to 1 mL/d (Mangum 1964b). Although these figures are similar, comparison is difficult as the size of the *Clymenella* used is not known. Since such a specimen of *A. catenata* can move 402 ± 55 mL of sediment per year, the relatively dense population of this species in St. Margaret's Bay, together with *P. gracilis* and *N. lumbricalis* which are also present, must play an important part in the turnover of the surface layers of sediment.

Axiothella catenata, *P. gracilis*, and *N. lumbricalis* all appear to be unselective in the ingestion of sediment from their habitat but Rhoads and Stanley (1965), found that the similar sized *Clymenella*, which lives in coarser sediment, was unable to ingest particles larger than 1 mm owing to the size of the mouth. The same would probably be true of *A. catenata*, *P. gracilis*, and *N. lumbricalis* if they, too, were living in sediment coarser than that in St. Margaret's Bay. The possibility that the lack of selectivity below the limit imposed by the size of mouth could make maldanids more sensitive to sediment type is unlikely as they are found in a variety of sediments (Mangum 1964a). Other factors such as the amount of organic matter in the sediment, particularly the portion readily digested by these animals, as suggested by Bader (1954), may prove more important in determining their abundance and distribution.

Acknowledgments

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A Bacterium Associated with Disease of Pond Cultured Channel Catfish, *Ictalurus punctatus*

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HAWKE, J. P. 1979. A bacterium associated with disease of pond cultured channel catfish, *Ictalurus punctatus*. J. Fish. Res. Board Can. 36: 1508–1512.

A new bacterial disease affecting primarily pond reared fingerling channel catfish, *Ictalurus punctatus*, is described from 17 instances reported from June 1976 through December 1978. Terramycin medicated feed controlled the disease when early diagnosis was possible. Terramycin resistant strains were not detected. The causitive organism was confirmed as a previously unidentified species of *Edwardsiella* by the Center for Disease Control, Atlanta, Georgia. The disease is referred to as Enteric Septicemia of Catfish (ESC). Optimum growth temperature is between 25 and 30°C; this correlated with pond water temperatures during instances of mortality on fish farms. Koch's postulates were fulfilled using channel catfish fingerlings in 40-L aquaria.

Key words: Fish disease, bacterial fish pathogen, enteric bacteria, channel catfish diseases

HAWKE, J. P. 1979. A bacterium associated with disease of pond cultured channel catfish, *Ictalurus punctatus*. J. Fish. Res. Board Can. 36: 1508–1512.

Le présent article contient une description d'une nouvelle maladie bactérienne affectant surtout les fingerlings élevés en étangs de barbue de rivière, *Ictalurus punctatus*, et fondée sur 17 cas signalés de juin 1976 à décembre 1978. Dans les cas où la maladie fut diagnostiquée assez tôt, il a été possible de contrôler la maladie grâce à un régime alimentaire traité à la terramycine. On n'a pas décelé de lignées résistantes à la terramycine. Le *Center for Disease Control* d'Atlanta en Georgie a identifié l'organisme pathogène comme espèce jusqu'à maintenant inconnue d'*Edwardsiella*. On a donné à la maladie le nom de septicémie entérique de la barbue (ESC, «Enteric Septicemia of Catfish»). La température optimale de croissance se situe entre 25 et 30°C; ceci correspond aux températures de l'étang au moment où l'on a signalé des mortalités dans les étangs de ferme. Les postulats de Koch ont été satisfaits avec des fingerlings de barbue de rivière dans des aquariums de 40 L.

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THIS note describes a bacterial disease primarily of cultured channel catfish, *Ictalurus punctatus*. Morphological and biochemical characteristics indicate that the causative organism is a member of the Enterobacteriaceae and is closely related to *Edwardsiella tarda*. Bacterial diseases of channel catfish have been reviewed extensively (Bullock et al. 1970; Rogers 1971; Meyer 1975; and Plumb 1975). Bacterial diseases of channel catfish may be caused by *Pseudomonas flourescens, Aeromonas hydrophila, Flexibacter (Chondrococcus) columnaris* and *Edwardsiella tarda*. All of these are motile gram negative rods. *Flexibacter columnaris* causes perhaps the most serious bacterial disease and may cause high losses during periods when fish are stressed. "Columnaris" disease occurs most frequently as an external infection. *Aeromonas hydrophila* and *P. flourescens* are involved in the complex of bacterial species which cause "hemorrhagic septicemia." *Edwardsiella tarda* causes a systemic infection known as "emphysematous putrefactive disease." Channel catfish virus disease (CCVD) is often accompanied by secondary bacterial infections of *A. hydrophila* or *F. columnaris* which may further increase losses (Fijan et al. 1970) (J. A. Plumb personal communication 1978).

The incidence of enteric bacteria causing disease in fish has been reported by Ross et al. (1966), Meyer and Bullock (1972), White et al. (1973) and is discussed in "Pathology of Fishes" Chap. 2, Ribelin and Migaki (1975). In these reviews it is clear that very few members of the Enterobacteriaceae are known to cause disease in fish.

Materials and methods — Source of isolates — Isolates were obtained in routine casework by the Southeastern Cooperative Fish Disease Project at Auburn University. The first case was received July 8, 1976 and the most recent October 17, 1978. Samples of tissue from the kidney, liver,

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spleen, intestine, brain, and skin/muscle lesions, if present, were aseptically plated on brain heart infusion (BHI) agar (Difco) plates and blood agar (BA) utilizing 5% whole human blood. Isolated colonies were restreaked and maintained on BA.

Identification procedure — Characterization of the organism was carried out by examining biochemical and morphological data obtained at Auburn University and at various other fish disease and microbiology laboratories. Morphology was examined using the Gram's stain and Leifson's flagella stain. Motility was determined in wet amounts observed with phase contrast microscopy (400×) and in semisolid glucose motility deeps (GMD) (Walters and Plumb 1978). Biochemical tests were carried out as follows; hydrogen sulfide (H_2S) production in triple sugar iron (TSI) agar (Difco) and motility sulfide (MS) agar (Difco); urease in urea broth (Difco); indole production in 1% tryptone water; nitrate reduction in nitrate broth after 3 d; oxidase test by the method of Kovacs, analytab 20E and 50R microtube tests (Analytab Products Incorporated) and the minitek system (BBL). Specific antisera for *E. tarda*, *A. Hydrophila* and *Yersinia ruckeri* (ERM) were obtained from the National Fish Health Laboratory, Leetown, West Virginia and were used to perform slide agglutination tests on cell suspensions of the various isolates. Determination of GC ratio by bouyant density was carried out by Dr D. H. Lewis, Texas A&M University.

All specimens were screened for channel catfish virus disease (CCVD) using a channel catfish ovary cell culture (P. R. Bowser and J. A. Plumb personal communication 1978).

Infectivity studies were conducted in 40-L aquaria. Twenty channel catfish fingerlings (10 cm average TL) were exposed to the pathogen by intraperitoneal injection with a 0.1 mL inoculum containing approximately 1×10^8 viable cells. Twenty (2 cm average TL) fingering channel catfish were infected by adding 3 mL of a bacterial suspension containing approximately 1×10^8 colony forming units (cfu)/mL of the organism directly to the aquarium water. Ten (13 cm average TL) channel catfish fingerlings were infected in a similar manner.

Viability studies were conducted in flasks containing 1600 mL of sterile pond water. A 1-mL bacterial suspension calibrated to a No. 3 McFarland tube was used to inoculate the flask which was incubated at room temperature on a mechanical shaker. Attempts at recovering the organism after 1, 4, 6, 8, 10, 12, and 15 d of incubation were made by platings on BHI agar.

Determination of optimum growth temperature (OGT) was done by inoculating glucose motility deeps (GMD) by vertical stabbing with a needle and incubating for 96 h at temperatures of 4, 10, 12, 15, 20, 25, 35, and 40°C. The (OGT) was considered that temperature where motility, acid, and gas production were most pronounced.

Antimicrobic susceptibility of each isolate was determined by the agar diffusion method (Bauer and Kirby et al. 1966) but sensitivity agar (Difco) was used rather than Mueller–Hinton (M–H) agar due to poor growth of isolates on M–H agar.

Two groups of three adult channel catfish (25 cm average TL) were injected with bacterins to determine the antigenic similarity of GA 7752 and *Edwardsiella tarda*. The fish were bled at the conclusion of a 6-wk injection schedule. Serum from each group was pooled and refrigerated at 4°C. Control serum was obtained from preinjection bleedings. Slide agglutination procedures were carried out using 2-fold dilutions of antiserum mixed with an antigen suspension calibrated to a No. 10 McFarland tube.

Results — Clinical signs of the disease are not consistent. Behavioral characteristics of fish in the final stages of the disease include: hanging listlessly at the surface tail down, spinning rapidly in circles, spiraling, or spinning followed soon thereafter by death. Gross external characteristics, which are occasionally absent particularly in specimens over 15 cm, are: petechial hemorrhages of the skin around the throat and mouth, pale gills, exophthalmia, an open lesion in the fontanelle of the frontal bone of the skull, and small cutaneous lesions on the lateral body surface. Gross internal characteristics are: hypertrophy of the kidney and spleen, areas of hemorrhage and necrosis in the liver, bloody ascitic fluid in the peritoneal cavity and petechial hemorrhages widespread in the adipose tissue, inner walls of the visceral cavity, dorsal musculature, and intestine. In smaller fish the disease may be easily confused with CCVD.

Physical and biochemical characteristics of the bacterium — Colonies of the bacterium on BHI agar are smooth, circular, and slightly convex with entire edges. Growth is slow and requires 48 h at 26°C to form typical 2 mm colonies. The gram negative cells measured 0.75×2.5 μm, and are weakly motile with peritrichous flagellation. The bacterium is cytochrome oxidase negative, fermentative in glucose O/F medium, reduces nitrate to nitrite, and does not produce a pigment, so it is considered to be a member of the Enterobacteriaceae.

Biochemical characteristics of the strains isolated from various geographic areas are consistent (Table 1). In many respects, the organism is similar to *E. tarda* (Ewing et al. 1965). *Edwardsiella tarda* is pathogenic to adult channel catfish (Bullock and Meyer 1973), eels (Wakabayashi and Egusa 1973), and largemouth bass (White et al. 1973). The organism described here is also biochemically similar to the ERM bacterium *Yersinia ruckeri*.

The organism described here differs from *E. tarda* in that it is negative for H_2S, indole, motility at 37°, gas from glucose at 37°, Jordan's tartrate and is not agglutinated by *E. tarda* antiserum. The organism differs from *Y. ruckeri* in that it is positive for motility at 25°C and gas from glucose at 25°C, and negative for citrate (Simmon's), trehalose, gelatin (22°C), and Jordan's tartrate (Table 2). The degree of relatedness of the causative organism of ESC and other members of the Enterobacteriaceae was determined by DNA homology. *Edwardsiella tarda* was found to be the most closely related species with 27–30% relatedness (D. Brenner personal communication 1979). Based on this information the ESC organism is considered to be a new species of the genus *Edwardsiella*. The organism is referred to by the type culture no. GA7752.

In antimicrobic susceptibility tests (Table 3), all strains of the organism were found to be sensitive to Terramycin, Furacin, Aureomycin, Streptomycin, Kana-

mycin, and Neomycin, but resistant to Sulfamerazine and Erythromycin.

All fish exposed to the bacterium by injection were dead 96 h postinjection. Many of the typical clinical signs of the disease were not apparent due to rapid death of the fish. In fish exposed to the organism by waterborne challenge, mortality was 100% in both groups of fish after 2 wk. During these tests, disease did not occur in control specimens.

Recovery of the organism from sterile pond water was successful up to 8 d postinoculation. After this time the organism could not be isolated from water samples taken at weekly intervals. No additional samples were taken after 1 mo of incubation.

No cross-reactivity was detected in a cross-agglutination experiment between *E. tarda* antiserum and bacterium 7752 antigen, and vice-versa. A titer of 160 was obtained with *E. tarda* antigen + antiserum and a titer of 320 was obtained with bacterium 7752 antigen + antiserum.

TABLE 1. Biochemical reactions of 16 strains of bacterium 7752 compared with those of *E. tarda*, *Paracolobactrum anguillimortiferum*, and *Yersinia ruckerii* (ERM).

Morphological or biochemical character	GA7752[a]	*E. tarda*[b]	*P. anguillimortiferum*[c]	*Yersinia ruckeri*[d] (ERM)
Gram stain	−	−	−	−
Motility 22°C	+	+	+	+
Motility 37°C	−	+	+	−
Flagellation	Peritrichous	Peritrichous	Peritrichous	Peritrichous
H_2S on TSI	−	+	+	−
Urease	−	−	−	−
Indole	−	+	+	−
MR/VP	+/−	+/−	+/−	+/−
Citrate (Simmon's)	−	−	0[e]	+
Citrate (Christensen's)	−	+	0	+
Citrate (Minitek)	−	+	0	
KCN		−	0	+
Gelatin	−	−	−	+
Arginine	−	−	0	−
Lysine	+	+	0	+
Ornithine	+	+	0	+
Ornithine (Minitek) 48 h	−	+	0	0
Phenylalanine	−	−	0	−
Glucose	+	+	+	+
Gas from glucose (22°C)	+	+	+	−
Gas from glucose (37°C)	−	+	+	−
Lactose	−	−	−	−
Sucrose	−	−	−	−
Mannitol	−	−	−	+
Dulcitol	−	−	−	−
Salicin	−	−	−	−
Adonitol	−	−	0	−
Inositol	−	−	0	−
Sorbitol	−	−	−	−
Arabinose	−	−	−	−
Raffinose	−	−	−	−
Rhamnose	−	−	−	−
Malonate	−	−	−	−
Maltose	+	+	+	+
ONPG	−	−	0	+
Oxidase	−	−	0	−
Xylose	−	−	−	−
Trehalose	−	−	−	+
Glycerol	+/−	(+)	(+)	(+)
Litmus milk	F	−	−	
Starch	0	−	−	0

[a]All strains of this organism were biochemically identical.
[b]Ewing et al. (1965).
[c]Wakabayashi et al. (1973).
[d]Ross et al. (1966).
[e]Data not available.

TABLE 1 (*Concluded*)

Morphological or biochemical character	GA7752[a]	*E. tarda*[b]	*P. anguillimortiferum*[c]	*Yersinia ruckeri*[d] (ERM)
Fructose	+	+	+	+
Galactose	+	+	+	+
Mannose	+	+	+	+
Sorbose	−	0	0	0
Erythritol	−	−	0	−
Ribose	+	0	0	0
Amygdalin	−	0	0	0
Arbutine	−	0	0	0
Esculin	−	−	−	−
Cellobiose	−	−	−	−
Inuline	−	−	−	0
Melitzitose	−	0	0	0
Dextrine	−	−	d	0
Amylose	−	0	0	0
DNAase	−	0	0	0
Pigment	−	−	−	−
Nitrate red.	+	+	+	+

TABLE 2. Selected diagnostic features of three enteric fish pathogens.

Biochemical character	GA7752	*E. tarda*	*Yersinia ruckeri* (ERM)
Motility 25°C	+	+	−
Motility 37°C	−	+	−
Cyt. ox.	−	−	−
O/F	+/+G	+/+G	+/+
TSI	K/AG	K/AG	K/A
Indole	−	+	−
Citrate (Simmons)	−	−	+
Trehalose	−	−	+
Gelatin (22°C)	−	−	+
Jordans tartrate	−	+	+
Gas from glucose 25°C	+	+	−
Gas from glucose 37°C	−	+	−
H_2S	−	+	−
G/C	53[a]	56–59	45–47

[a](D. H. Lewis 1978) personal communication.

TABLE 3. Antimicrobial sensitivity of 10 strains of bacterium 7752 compared to *E. tarda*. (Wakabayashi and Egusa 1973).

Antimicrobial agent	Level of sensitivity[a] GA7752	*E. tarda*
Terramycin	++++	+++
Aureomycin	+++	NA
Erythromycin	R	R
Kanamycin	++	+++
Neomycin	++	NA
Nitrofurazone	+++	NA
Dihydrostreptomycin	++	+++
Sulfamerizine	R	R

[a]Indicates zone of inhibition in cm, 0–0.9 (+), 1–1.9 (++), 2–2.9 (+++), 3–3.9 (++++); NA — Data not available; R — Resistant.

Discussion — The disease can be classified as an acute septicemia that progresses rapidly in apparently healthy fast-growing fish. All fish examined were robust and had ample visceral fat. Prior to losses only a slight decrease in feeding activity was noted by farm owners.

In experiments to determine the optimum growth temperature, the organism grew best at 25°C and not at all below 12°C or above 37°C (Table 4). Most fish farmers interviewed stated that the average water temperature during periods of mortality was approximately 26°C.

Mortality in most instances was controlled in 4–7 d by feeding Terramycin medicated feed at 2.5 g active ingredient 45.4 kg fish/d. In two instances the mortality was reduced greatly but could not be brought completely under control.

The range of the organism is unknown. All diseased

TABLE 4. Growth of bacterium 7752 at various temperatures in glucose motility deeps (GMD). at 96 h incubation.

Incubation temp.	Action in GMD			
	Growth	Motility	Acid prod.	Gas prod.
4°C	–	–	–	–
10°C	–	–	–	–
12°C	–	–	–	–
15°C	+	(+)[a]	(+)	–
20°C	+	+	+	+
25°C	+	+	+	+
30°C	+	+	+	(+)
35°C	+	–	+	(+)
40°C	–	–	–	–

[a](+) = Weak positive reaction.

specimens were voluntarily sent to the SECFDL by farmers or biologists in the cooperating states. A survey to determine the range of the disease has not been conducted. At present the disease constitutes an economic threat particularly to farmers in central Alabama and Georgia. I feel the disease could have a detrimental effect on catfish culture anywhere in the United States provided water temperatures are favorable for its development.

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Intercomparison of Niskin and Blumer Samplers for the Study of Dissolved and Dispersed Petroleum Residues in Seawater

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LEVY, E. M. 1979. Intercomparison of Niskin and Blumer samplers for the study of dissolved and dispersed petroleum residues in seawater. J. Fish. Res. Board Can. 36: 1513–1516.

A comparison of the data from Niskin and Blumer contamination-free samplers regarding the concentration of dissolved and dispersed petroleum residues in seawater demonstrated that equivalent information may be obtained if the appropriate procedures are used.

Key words: petroleum, pollution, seawater, samplers

LEVY, E. M. 1979. Intercomparison of Niskin and Blumer samplers for the study of dissolved and dispersed petroleum residues in seawater. J. Fish. Res. Board Can. 36: 1513–1516.

La comparaison de données, recueillies par des appareils Niskin et Blumer non souillés, sur la teneur en résidus pétroliers dissous et dispersés dans l'eau de mer montre que les résultats sont comparables si l'on procède de la manière appropriée.

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DURING the past few years, the role of organic substances as marine pollutants has become increasingly appreciated and considerable research has been directed towards those compounds and marine media for which acceptable sampling and analytical procedures are available. Adequate methods, however, generally do not exist for most organic substances in the water column where concentrations are usually extremely low and where samples must be procured remotely with a sampling device which is always a potential source of contamination. Sampling problems are rendered even more difficult when the organic substances are not homogeneously distributed and may be present in true solution, dispersed as micelles, associated with suspended inorganic particles, or concentrated in the surface microlayer.

Most of the conventional devices for collecting water samples at various depths in the ocean are designed for lowering in an open configuration to the desired depth where the sampler is closed. During its descent, the inner walls of the sampler pass through the surface microlayer, where high concentrations of surface-active organic substances may have accumulated, and then through the overlying water column. Substances present in these waters may be adsorbed onto the inner walls of the sampler and subsequently desorbed to contaminate the water sample. This is generally thought to be the most serious source of contamination in studies of petroleum residues in the water column. To assess the effect that it might have had on data collected during studies of the distribution of dissolved and dispered petroleum residues in the waters of the North Atlantic (Levy 1971, 1972, 1979; Levy and Walton 1973), two experiments were carried out to compare data obtained by the methods used previously and those collected with a contamination-free Blumer sampler (Clark et al. 1967).

Experimental — Experiment 1 — This was carried out from CSS *Dawson* in the Gulf Stream/Sargasso Sea area in May, 1977 (Cruise 77-010). Conventional 5-L and 12-L Niskin samplers separated by about 1 m were attached to a hydrowire about 1 m above the 15-L Blumer sampler. A lead weight overcame the buoyancy of the empty sampler and prevented the cast from "kiting" as it was lowerd. To ensure implosion of the rupture disk, the cast was lowered to a depth where the pressure rating of the disk was exceeded by 10%. Both filtered (precombusted glass fibre filters) and unfiltered samples were taken with the Blumer sampler. Samples were collected at depths ranging from 100 to 3500 m.

On retrieval of the cast, 1-L subsamples were drawn from the Niskin samplers and extracted twice with carbon tetrachloride according to previous procedures (Levy 1977). Samples were also drawn for salinity to determine whether all three samplers had sampled the same body of water.

The entire contents of the Blumer sampler were extracted with carbon tetrachloride in an all-glass-and-teflon two-stage extractor (Fig. 1). The seawater was forced by inert gas pressure from the glass bottle of the Blumer sampler via a constant pressure device into the first stage of the extractor. This was made from a 2-L Erlenmeyer flask with appropriately located inlet and drain cocks. When the flask had filled with water the speed of the magnetic stirrer was adjusted so that the carbon tetrachloride (200 mL) was broken up into very small droplets and evenly dispersed throughout the flask. Most of the carbon tetrachloride suspension which escaped through the neck of the flask settled out

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TABLE 1. Comparison of data from Niskin and Blumer samplers — Experiment 1.

Station no.	Latitude	Longitude	Depth (m)	Salinity (‰)			Petroleum residues ($\mu g \cdot L^{-1}$)		
				Blumer	5-L Niskin	12-L Niskin	Blumer	5-L Niskin	12-L Niskin
1	44–05.1	63–08.6	100	33.669	33.815	34.023	0.43[a]	1.75	4.50
2	39–55.3	54–05.2	3200	35.014	35.036	—	0.63[a]	2.50	—
3	38–13.2	50–05.7	2300	34.955	34.974	34.975	0.27[a]	0.60	0.50
4	37–59.4	49–37.3	3500	34.931	34.931	34.931	0.33[a]	1.00	1.00
5	38–18.5	49–55.1	3500	34.927	34.925	34.928	0.27	0.50	1.50
6	39–13.0	50–12.1	2300	34.955	34.971	34.968	0.63	0.40	0.40
7	39–10.0	52–49.3	1700	34.953	34.977	34.978	0.30	1.00	0.45
8	39–35.8	53–36.1	1700	34.952	34.985	34.988	0.27[a]	0.15	0.15
9	40–38.4	54–47.2	500	35.508	35.535	35.526	0.17[a]	0.20	0.45
10	40–51.1	55–26.8	—	—	35.985	35.995	0.50	0.75	0.55

[a]Water sample filtered.

in a 500-mL chamber where the linear flow was decreased temporarily. The water then passed into the second stage where the extraction was repeated. The flow was 250 $mL \cdot min^{-1}$ so that the "residence time" in each extractor was about 8 min. The carbon tetrachloride was recovered from the apparatus and placed in an amber glass bottle. Loss of carbon tetrachloride was negligible. At several stations portions of carbon tetrachloride were taken as blanks. The extracts were processed and analyzed by fluorescence spectrophotometry according to the customary procedures (Levy 1977).

Experiment 2 — This was carried out during CSS *Hudson* cruise (77-024) to the Arctic during the summer of 1977. A comparison was made between samples collected with conventional 5-L Niskin samplers in a CTD/Rosette assembly and those taken with the Blumer sampler on a separate cast. The Rosette was lowered to within a few metres of the bottom and the samplers were closed at the desired depths during retrieval. As a result, many volumes of water passed through the samplers during their passage through the water column — in many cases more than a 1000 m — and any sea surface materials which were adsorbed on the sampler walls sufficiently strongly to withstand this very thorough rinsing should remain there and not contaminate the water sample.

The water was processed as described for Experiment 1.

Results and discussion — Experiment 1 — As indicated in Table 1, excessive differences in the salinities of the samples taken at Station 1 (a maximum spread of 0.354‰ as compared with the average of 0.018‰) demonstrated that there was either a malfunction of the Niskin samplers or that the Blumer bottle had not been completely filled before beginning to retrieve the cast. Since precisely the same water was not sampled by all three samplers, the petroleum residue concentrations at this station cannot be used to evaluate the performance of the samplers. On the other hand, the salinity data indicate that the data taken at the remaining stations are reliable and that valid comparisons of the petroleum residue concentrations are possible.

The *t*-tests for paired observations (Table 2) demonstrated that there was no difference between the salinities obtained from the 5-L and 12-L Niskin samplers and therefore the average of these was taken for comparison with the salinity from the Blumer sampler. Although a statistically significant difference was observed, this is a reflection of the high precision with which salinity can be measured and is not important from the point of view of environmental quality. Similarly, the dif-

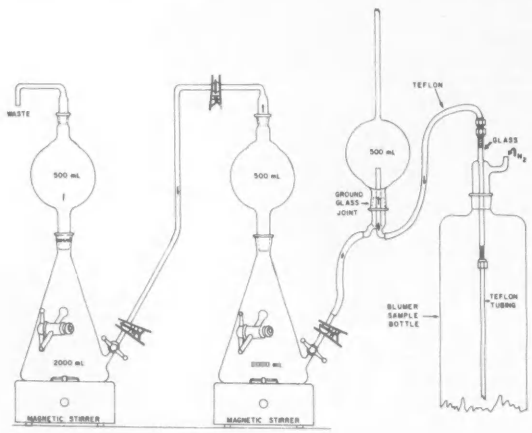

FIG. 1. Extraction apparatus.

TABLE 2. Statistics related to data from Experiment 1.

Statistic	Salinity		Petroleum residues	
	5-L vs. 12-L	Avg vs. Blumer	5-L vs. 12-L	Avg vs. Blumer
σ_d	0.005	0.012	0.45	0.63
$\bar{D}$	0.001	0.017	0.05	0.44
γ	7	7	7	8
t_{calc}	0.39	4.06	0.32	2.10
$t_{0.95}$	2.37	2.37	2.37	2.31

TABLE 3. Comparison of data from Blumer and Niskin samplers — Experiment 2.

Station no.	Latitude	Longitude	Blumer sampler		Niskin sampler	
			Depth (m)	Concentration ($\mu g \cdot L^{-1}$)	Depth (m)	Concentration ($\mu g \cdot L^{-1}$)
18	73–27.3	67–17.3	1800	0.58	1500/2000	0.40, 0.40
19	72–14.1	65–56.9	1800	0.68	1500/2000	0.40, 0.35
21	71–16.0	70–27.0	250	0.17	200/410	0.80, 0.30
54	78–20.4	73–39.8	400	0.47	300/400/465	0.20, 0.20, 0.35
				σ_d 0.31		
				$\bar{D}$ 0.08		
				γ 3		
				t 0.527		
				$t_{0.95(3)}$ 3.18		

ferences between the petroleum residue concentrations from the 5-L and 12-L Niskin samplers were not statistically significant and the average was taken for comparison with the concentration observed in the Blumer sample. Again, the differences in data obtained with the two types of samplers were neither statistically nor environmentally significant.

The data obtained with the Blumer sampler were considerably more uniform than those from the Niskin samplers because of the improvement in analytical sensitivity and precision achieved by processing a larger volume of water. Most of the Niskin sampler data were near the limit of the analytical method and this accounts for the variability between the 5-L and 12-L Niskin samplers. Although the lower limit of the method can be extended by processing larger volumes of water, as demonstrated by the data from the Blumer sampler, this has not been found to be necessary for studies of background levels of petroleum residues in the open ocean.

Experiment 2 — Because of the effect of temperature and salinity on ambient pressure, there was some uncertainty in the depth at which the Blumer samples were collected, and since separate casts were necessary, a slight difference in water properties might be anticipated. Accordingly, the concentration data for the samples collected with the Blumer sampler were compared with the average concentrations of samples taken with Niskin bottles at the standard oceanographic depths immediately above and below the calculated depth of rupture. This should not be a significant source of ambiguity since there was no indication from the depth profiles that the concentrations of dissolved and dispersed petroleum residues in Baffin Bay varied in a meaningful manner with depth below the immediate surface layers (Levy 1979). In three of the four sets of data, concentrations in the samples collected with the Blumer sampler were higher than those collected with the Niskin samplers. As in the previous experiment, the small differences in concentration obtained by the two sampling and analytical procedures were not statistically significant. This provides strong evidence that the latter were not contaminated by substances inadvertently collected from the surface microlayer or from the near-surface waters of the ocean. In addition, the data demonstrate that the PVC samplers themselves were not a significant source of interference in the procedures used.

Conclusions

Two experiments to evaluate the hazard of sample contamination when studying dissolved and dispersed petroleum residues in the water column demonstrated that there were no gross contamination problems with either Niskin or Blumer samplers when deployed properly. Data collected with the Blumer sampler generally showed less variability and perhaps were slightly more reliable at the very low background levels of these substances in the open ocean. However, since the data collected with Niskin samplers can be fully as reliable as those obtained from the Blumer contamination-free sampler, the choice becomes largely one of economy and convenience for routine work at sea. Consequently, Niskin samplers are the obvious choice, preferably used in a Rosette, if a variety of depths are to be sampled and large numbers of samples are to be collected in a limited period of time. Provided reasonable precautions are taken not to deploy them where there is a heavy oil slick on the sea surface, Niskin samplers can be used with confidence in measuring background levels of dissolved and dispersed petroleum residues in the open ocean.

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Assimilation Efficiency of Dietary Methylmercury by Northern Pike (*Esox lucius*)

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PHILLIPS, G. R., AND R. W. GREGORY. 1979. Assimilation efficiency of dietary methylmercury by northern pike (*Esox lucius*). J. Fish. Res. Board Can. 36: 1516–1519.

Northern pike (*Esox lucius*) retained an average of 19% (range 6–31%) of the methylmercury which they ingested during consumption of young-of-the-year carp (*Cyprinus carpio*) collected from a pond; carp accumulated methylmercury naturally while in the pond. The total amount of mercury in pike increased with time (up to 42 d) but concentration in the tissue decreased due to growth dilution; duration of ingestion did not influence efficiency of methylmercury assimilation. This value (19%) is considerably lower than most efficiencies reported in the literature, demonstrating that methylmercury in this forage fish is less readily available to a predator fish than previous studies implied.

Key words: bioaccumulation, mercury compounds, predators, Esocidae

PHILLIPS, G. R., AND R. W. GREGORY. 1979. Assimilation efficiency of dietary methylmercury by northern pike (*Esox lucius*). J. Fish. Res. Board Can. 36: 1516–1519.

Le grand brochet (*Esox lucius*) a retenu en moyenne 19% (variation de 6 à 31%) du méthylmercure ingéré après avoir consommé de jeunes carpes de l'année (*Cyprinus carpio*) tirées d'un étang. Durant leur séjour dans l'étang, les carpes concentraient naturellement le méthyl-mercure dans leurs tissus. La quantité totale de mercure présente dans le brochet a augmenté dans le temps (jusqu'à 42 jours), mais la teneur a diminué du fait de la croissance. La durée d'ingestion n'a pas influé sur le taux d'assimilation du méthyl-mercure. Ce taux (19%) est considérablement plus bas que la plupart de ceux qui sont signalés dans la documentation, ce qui montre que le méthyl-mercure accumulé dans la carpe n'est pas aussi facilement assimilable par un poisson prédateur que le laissaient croire les recherches antérieures.

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METHYLMERCURY has been extensively studied in aquatic environments, primarily because of the risks involved with human consumption of contaminated fish. Recently, workers in Sweden (Fagerstrom and Asell 1973; Fagerstrom et al. 1974) and in Canada (Norstrom et al. 1976) have attempted to model the accumulation of methylmercury by fishes; these models distinguish between methylmercury derived from water or from the diet. Although the models differ, a common feature is that the food component of methylmercury uptake is viewed as being proportional to the efficiency with which methylmercury is extracted from the diet.

Norstrom et al. (1976) have chosen a coefficient of 0.8 (80%) to describe dietary methylmercury assimilation based on the work of a variety of investigators (Hannerz 1968; de Freitas et al. 1974; Suzuki and Hatanaka 1975) while Fagerstrom and Asell (1973) have used a value of 0.15 (15%) after the work of Jernelov (1968). Because of the disparity of these co-

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efficients, this study was initiated to obtain more conclusive evidence on the efficiency with which a predator fish could assimilate methylmercury from a prey organism collected from nature.

Materials and methods — Northern pike (*Esox lucius*) obtained from a federal hatchery (U.S. Fish and Wildlife Service, Garrison Dam National Fish Hatchery, Riverdale, North Dakota) were fed young-of-the-year carp (*Cyprinus carpio*) collected from a pond located within the flood plain of the Tongue River, near Decker, Montana. Carp had accumulated methylmercury naturally while in the pond.

Pike were kept in four fiberglass living streams (Frigid Units, Inc., Toledo, Ohio) each of which was partitioned into four identical (400 L) compartments; two fish were housed in each compartment. Pike were fed rainbow trout (*Salmo gairdneri*) obtained from a local hatchery (U.S. Fish and Wildlife Service's Fish Cultural Development Center, Bozeman, Montana) during a 10-d acclimation period prior to the 42-d test. During the test pike were offered carp at an average rate of 9% wet weight/d. Pike were individually weighed and marked (fin clipped) at the onset; they were killed in groups of eight and subsequently analyzed for mercury after 13, 29, and 42 d. Surviving pike were reweighed at the killing intervals and their rations were readjusted to fixed percentages of body weight after each weighing. Eight pike were also killed for mercury analyses at the beginning of the test; the average mercury content of these (0.10 ± 0.01 μg Hg/g) was assigned as the initial mercury content of each experimental pike. Eight more control pike (fed rainbow trout during the test) were killed and analyzed at the end.

Since pike were fed in groups of two, the amount of food (and therefore, the amount of mercury) fed to each individual was estimated as being proportional to the growth of the two fish. Thus, if a pair of pike were fed 100 g of food and their individual weight increases were 20 and 30 g, it was estimated that they consumed 40 and 60 g of food, respectively.

Groups of 10–15 carp were analyzed for total mercury 19 times during the test as were five groups of rainbow trout; results were used to calculate the amount of mercury fed to pike. This quantity was derived for fish killed after each interval from the total weight of carp fed and the average mercury content of carp analyzed up to that date. The mean mercury concentrations (μg Hg/g) in carp fed to pike over the three sacrifice intervals were 0.14, 0.12, and 0.10, respectively. Rainbow trout averaged 0.01 μg Hg/g. Seven of the experimental pike and three groups of carp were also analyzed for methylmercury to determine the percentage of mercury present in this form.

Mercury concentrations in fish tissue were determined from aliquots of whole fish homogenates. Homogenates were prepared by blending whole pike (or groups of whole carp or trout) and a few grams of dry ice in a high speed blender. Blende samples were warmed to room temperature, resulting in a homogeneous paste.

Total mercury was determined by using a Varian model AA-6 atomic absorption spectrophotometer equipped with a carbon rod atomizer (Siemer and Woodriff 1974). Precision was estimated at ± 0.01 μg Hg/g based on the standard deviation of repeated analyses of the same sample.

Methylmercury was determined by homogenizing the fish, washing with acetone, freeing the methylmercury with hydrochloric acid, partitioning the methylmercury into benzene, and finally quantifying using a Varian model GC-3700 gas–liquid chromatograph equipped with an electron capture detector (Watts et al. 1976). Error (determined from know standards) was relatively large (±30%) because the methylmercury concentrations analyzed were near the lower detection limit; this resulted in some percentages of methylmercury exceeding one hundred.

During the test, flow rates averaged 500 mL/min and photoperiod was 16 h light:8 h dark. Characteristics (mean) of the test water were: temperature 18.0°C, pH 8.31, dissolved oxygen 8.21 mg/L, total alkalinity (as $CaCO_3$) 69 mg/L, and hardness (as $CaCO_3$) 72 mg/L (APHA et al. 1976). Mercury was analyzed weekly in the test water but was never detected (lower detection limit 0.1 μg Hg/L).

Results and discussion — Control pike, fed rainbow trout during the test, did not accumulate mercury. The mean mercury content of the trout was 0.01 μg Hg/g and pike that were fed trout averaged 55.2 g and 0.02 μg Hg/g after 42 d compared to 10.9 g and 0.10 μg Hg/g at the beginning. Therefore, the average control fish contained 1.10 μg of Hg at the end of the test compared to 1.09 μg of Hg at the onset. Thus, it is reasonable to assume that mercury accumulated by pike during the experiment originated from their diet (carp) and not from water. Norstrom et al. (1976) estimated fractional clearance of methylmercury at 30%/yr. This is less than 3.5% over 42 d; thus, we assumed that clearance was negligible during this test.

In fish analyzed for both total mercury and methylmercury, methylmercury was the predominant mercurial present. Methylmercury accounted for 88, 98, 103, 115, 90, 112, and 111% of the mercury in pike and 80, 115, and 124% of the mercury in carp. Other workers have reported similar findings (Bache et al. 1971; Westoo 1973). Based on these results, we assumed that all of the mercury in pike and carp was methylmercury.

The concentration of mercury in the experimental fish decreased throughout the test (due to growth dilution) but the total amount of mercury in pike increased with time (Table 1). Pike assimilated, on the average, 20, 20, and 17% of the mercury they consumed after 13, 29, and 42 d, respectively; these values are not significantly different, even at the 60% level of confidence (Student's *t*-test). The overall average during the experiment was 19%. This percentage is near that reported by Jernelov (1968), who fed "biologically synthesized" methylmercury to a predator fish, but lower than most values (38–89%) reported in the literature (Table 2). The important point here is that most workers have computed dietary methylmercury assimilation efficiencies from experiments during which methylmercury was offered to fish in a production diet (Lock 1975; Sharp et al. 1977; Phillips and Buhler 1978), orally administered in a water solution or tissue homogenate (Miettinen et al. 1970), or was present in a prey fish that had been exposed to high levels of methylmercury in water for a short duration (Jernelov 1968; Suzuki and Hatanaka 1975). Methylmercury added to a fish's diet by any of the above methods could conceivably be

TABLE 1. Growth, food consumption, mercury consumption, and mercury accumulation by northern pike fed young-of-the-year carp collected from the field. Values are means ± 2 SE, ranges in parentheses.

Parameter measured	Sacrifice interval (d)			
	13	29	42	42 (control)
Pike weight (g)				
Initial	11.1 ± 1.3 (9.5–15.2)	11.2 ± 1.3 (9.9–14.9)	11.8 ± 1.2 (9.9–14.4)	10.9 ± 1.3 (9.7–14.6)
Final	17.0 ± 2.3 (12.7–22.9)	32.9 ± 3.3 (27.7–40.0)	55.7 ± 7.2 (44.9–73.6)	55.2 ± 6.7 (45.2–69.8)
Quantity of food fed (g)[a]	15.8 ± 3.5 (8.0–21.2)	55.8 ± 5.2 (46.6–66.0)	114.4 ± 17.4 (86.0–152.2)	110.0 ± 14.3 (92.5–153.1)
Mercury concentration in pike (μg Hg/g)				
Initial[b]	0.10 ± 0.01 (0.08–0.11)	0.10 ± 0.01 (0.08–0.11)	0.10 ± 0.01 (0.08–0.11)	0.10 ± 0.01 (0.08–0.11)
Final	0.09 ± 0.01 (0.08–0.12)	0.07 ± 0.01 (0.05–0.09)	0.06 ± 0.01 (0.03–0.08)	0.02 ± 0.01 (0.01–0.03)
Quantity of mercury in pike (μg Hg)				
Initial	1.12 ± 0.13 (1.00–1.52)	1.12 ± 0.13 (0.99–1.49)	1.18 ± 0.12 (0.99–1.44)	1.09 ± 0.09 (0.09–1.38)
Final	1.54 ± 0.18 (1.02–1.83)	2.42 ± 0.36 (1.66–3.19)	3.06 ± 0.46 (1.93–4.03)	1.10 ± 0.12 (0.95–1.48)
Change	0.43 ± 0.14 (0.07–0.76)	1.30 ± 0.33 (0.65–1.86)	1.87 ± 0.36 (0.94–2.64)	0.01 ± 0.07 (−0.21–0.17)
Quantity of mercury fed (μg Hg)	2.21 ± 0.49 (1.12–2.97)	6.69 ± 0.63 (5.52–7.92)	11.44 ± 1.74 (8.60–15.22)	—[c]
Mercury assimilated (%)	20 ± 7 (6–31)	20 ± 5 (9–29)	17 ± 4 (7–28)	—[c]

[a]Calculated as proportional to individual weight changes of pairs of northern pike that were kept in the same compartment.
[b]Based on the average mercury concentration of eight fish that were sacrificed at the onset.
[c]These values were not calculated because both the change in the quantity of mercury in control pike and the concentration of mercury in the control diet were, for all practical purposes, zero.

loosely bound and therefore readily assimilated by a consumer fish, whereas methylmercury present in the diets of fish in nature may be associated with non-digestible components.

Archer et al. (1973) concluded that 80% of the methylmercury present in swordfish (*Xiphias gladius*) meat is bound to tissues resistant to digestion. Other metals, including strontium (Schiffman 1959) and zinc (Pentreath 1973) were reportedly less readily assimilated by fish from natural diets than from artificial diets. Thus, metals or metal derivatives such as methylmercury are probably less available to fish in nature than many studies indicate. Future models of dietary methylmercury assimilation should employ a coefficient in the 15–20% range.

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TABLE 2. The efficiencies with which various species of fish were reported to have assimilated methylmercury from their diet.

Fish species	Diet used	Origin of CH_3–Hg^+ in diet	% CH_3–Hg^+ assimilated	Reference
Goldfish (*Carrassius auratus*)	Tetrafin goldfish food	Added during diet formulation	71–89	Sharp et al. (1977)
Rainbow trout (*Salmo gairdneri*)	Trout pellets (brand not specif.)	Added during diet formulation	52–71[a]	Lock (1975)
Rainbow trout (*S. gairdneri*)	Oregon Test Diet	Added during diet formulation	68	Phillips and Buhler (1978)
Yeliowtail (*Seriora quinqueradiata*)	Anchovy (*Engraulis japonica*)	Prey fish exposed in laboratory	67	Suzuki and Hatanaka (1975)
Northern pike (*Esox lucius*)	Orally administered water solution	Dissolved in solution	55	Miettinen et al. (1970)
Predator fish (not specified)	Prey fish (not specified)	Prey fish exposed in laboratory[b]	40–45	Jernelov (1968)
Northern pike (*E. lucius*)	Orally administered cow liver homogenate	Added during blending	38	Miettinen et al. (1970)
Predator fish (not specified)	Prey fish (not specified)	Prey fish collected[b] from nature	10–15	Jernelov (1968)
Northern pike (*E. lucius*)	Carp (*Cyprinus carpio*)	Prey fish collected from nature	19	This study

[a]Data for fish that consumed a diet containing 3.4 μg Hg/g dry weight as methylmercury for 1–3 w.
[b]Origin of CH_3-Hg^+ in diet not actually stated but implied.

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Wax Esters in the Marine Environment: Origin and Composition of the Wax from Bute Inlet, British Columbia

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During severe winters large amounts of a solid lipid accumulate on the water surface and on the shores of Bute Inlet, a deep fjord on the mainland of British Columbia. Chromatographic analyses show that this wax consists chiefly of wax esters (48%), with minor amounts of hydro-

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carbons (4%) and triacylglycerols (6%). Dominant among the zooplankton in this inlet is the copepod *Calanus plumchrus*, which also is rich in wax esters (40–50% of dry weight). Except for the lack of polyunsaturation in Bute Inlet wax there is a close similarity between the wax ester, alcohol, and fatty acid compositions of *C. plumchrus* and Bute Inlet wax. The major hydrocarbon of both is pristane. We hypothesize that Bute Inlet wax is produced by some major change in water conditions which cause a massive kill of copepods. At winter temperatures this lipid is a solid and as such may accumulate on the beach. Copepods are the likely source for the wax esters in slicks and sediments reported from oceanic areas throughout the world.

Key words: marine pollution, biological pollutant, lipid, hydrocarbon, wax, zooplankton, Copepoda

LEE, R. F., AND J. C. NEVENZEL. 1979. Wax esters in the marine environment: origin and composition of the wax from Bute Inlet, British Columbia. J. Fish. Res. Board Can. 36: 1519–1523.

Durant les hivers rigoureux, des quantités importantes d'un lipide solide s'accumulent sur l'eau et les rives de l'inlet Bute, qui s'avance profondément dans les terres de la Colombie-Britannique. La chromatographie a révélé qu'il s'agissait d'une paraffine composée principalement d'esters (48%) et, dans une plus faible proportion, d'hydrocarbures (4%) et de triacylglycérols (6%). Or, le copépode *Calanus plumchrus*, espèce dominante du zooplancton de l'inlet, est riche aussi en esters (40 à 50% en poids sec). Mis à part le fait que la paraffine surnageante n'est pas polyinsaturée comme celle de l'insecte, les teneurs en esters, en alcools et en acides gras sont très voisines. Dans les deux cas, le principal hydrocarbure est le pristane. Nous pensons que la paraffine répandue dans l'inlet résulte d'une modification profonde de l'état des eaux, qui entraîne la destruction massive des copépodes. L'hiver, le lipide est solide et peut, par conséquent, s'accumuler sur le rivage. Les copépodes sont la source la plus probable des esters trouvés dans les nappes et les sédiments des régions maritimes du monde entier.

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BUTE Inlet, one of the deep fjords (650 m) of British Columbia, is the source of an unusual waxy material, referred to as Bute Inlet wax (Anon. 1951; Williams 1957; Adams and Bonnett 1969). This material accumulates only during the coldest winters, and we were told by Mr Len Parker, a resident of this inlet since 1923, that 15 gallons or more of the solid wax could be collected from a few hundred yards of beach in some years. This paper presents data supporting our hypothesis that copepods are the source of Bute Inlet wax. In particular, *Calanus plumchrus*, an important species of zooplankton in the Inlet, contains large quantities of wax esters (Lee et al. 1972).

During several cruises to Bute Inlet in the spring and fall of 1971 and 1972 aboard the R/V *Dolphin* (Scripps Institution of Oceanography) and the C.S.S. *Vector* (Environment Canada) we collected zooplankton from various depths, proceeding from the mouth to the head of Bute Inlet. We also had available a frozen sample of zooplankton collected from 200 m in February 1972, and two samples of Bute Inlet wax collected in Bear Bay (about 9 miles from the head of the inlet), one in 1951 and the other during the winter of 1970–71.

Methods — Zooplankton lipids were extracted with chloroform/methanol (2:1 v/v) and fractionated into component lipid types by chromatography on silicic acid columns (Lee et al. 1971). Gas–liquid chromatographic (GLC) analyses of the native wax esters, the long-chain alcohols (as trifluoroacetates) and the fatty acids (as methyl esters) were carried out as previously described (Lee et al. 1971). The positions of the double bonds in the C_{16}, C_{18}, C_{20}, and C_{22} monounsaturated alcohols and acids were determined by ozonolysis (Stein and Nicolaides 1962) after separation of the individual chain lengths by preparative GLC.

Results — The major lipid types present in both the 1951 and 1970–71 samples of Bute Inlet wax were wax esters (48%), with minor amounts of hydrocarbons (4%) and triacylglycerols (6%). Unidentified material which was more polar than sterols by thin-layer chromatography, but contained no phosphorus, accounted for 41% of the wax. On a silica gel G thin-layer plate this unidentified material gave a long streak from the origin to the solvent front, suggesting polymerized lipids from the autoxidation of polyunsaturated components.

The wax esters ranged in chain lengths (alcohols plus acids) from C_{28} to C_{44} (Table 1). This composition does not resemble plant cuticle (Tulloch 1976), insect (Jackson and Blomquist 1976), or mineral waxes (Warth 1947). The major alcohol components were 16:0, 16:1, 18:1, 20:1, and 22:1 (Table 2), in agreement with the previous work of Adams and Bonnett (1969).

The preadult stage, copepodid V, of *C. plumchrus* collected in the spring (June) and winter (February) had wax ester contents (dry weight basis) of 51 and

TABLE 1. Chain lengths of wax esters.

Carbon number (alcohol + acid)	Bute Inlet wax 1951	Bute Inlet wax 1971	*Calanus plumchrus* (spring sample)
	weight percent		
30	6	8	8
32	6	6	12
34	34	36	22
36	31	31	28
38	11	9	14
40	5	3	6
42	3	4	5

39%, respectively. The chain lengths and alcohol compositions of these copepod wax esters were very similar to those of Bute Inlet wax. The similarity between the two sources extends to the positions of the double bonds in the monounsaturated C_{16}-C_{22} alcohols (Table 2). Note the relative amounts of the various 20:1 and 22:1 isomers; the high proportions of molecules with the double bond at the 9, 10-position (i.e. 20:1 *n*-11 and 22:1 *n*-13) imply extensive desaturation of saturated C_{20} and C_{22} carbon chains, rather than chain elongation of existing shorter, monounsaturated chains. Known mammalian and plant desaturases act predominantly on C_{16} and C_{18} saturated fatty acids, introducing the double bond at the 9, 10-position (*n*-7 and *n*-9, respectively); subsequent chain elongation leads to *n*-7 and *n*-9 C_{20} and C_{22} monoenoic acids, with the latter position greatly predominating (Gurr and James 1971). Our more detailed work confirms the data of Adams and Bonnett (1971) for the structure of Bute Inlet wax monoenoic alcohols and fatty acids.

TABLE 2. Compositions of wax esters from Bute Inlet and *Calanus plumchrus*. Only the principal components are listed, rounded off to the nearest whole number. Alc: alcohol; FA: fatty acid; N.D.: not detected; T: trace (less than 0.5%).

Component	Bute Inlet wax		*Calanus plumchrus* Spring		*Calanus plumchrus* Winter	
	Alc	FA	Alc	FA	Alc	FA
	weight percent					
14:0	1	53	3	22	2	11
16:0	3	17	11	17	5	14
16:1 *n*-5	T	1	T	8	6	10
16:1 *n*-7	8	5	9			
16:2	N.D.	N.D.	N.D.	3	N.D.	1
16:3	N.D.	N.D.	N.D.	8	N.D.	1
16:4	N.D.	N.D.	N.D.	1	N.D.	2
18:0	T	N.D.	T	T	1	T
18:1 *n*-7	T	1	1	T	4	2
18:1 *n*-9	4	2	3			
18:2	N.D.	N.D.	N.D.	6	N.D.	T
18:3	N.D.	N.D.	N.D.	3	N.D.	T
18:4	N.D.	N.D.	N.D.	6	N.D.	3
20:1 *n*-9	6	2	7	3	35	19
20:1 *n*-11	39	7	31			
20:4	N.D.	N.D.	N.D.	4	N.D.	T
20:5	N.D.	N.D.	N.D.	8	N.D.	15
22:1 *n*-9	1	T	T	N.D.	41	14
22:1 *n*-11	19	6	28			
22:1 *n*-13	17	1	4			
22:6	N.D.	N.D.	N.D.	4	N.D.	2

The wax ester fatty acids of *C. plumchrus* were high in polyunsaturation in contrast to Bute Inlet wax, which contained only saturated and monounsaturated components (Table 2). Long exposure of Bute Inlet wax to air would allow oxidation processes to destroy polyunsaturated fats, giving rise to polymers as discussed above. The spring and winter samples of *C. plumchrus* were 44 and 23% polyunsaturated, respectively. The higher proportion of 20:1 and 22:1 fatty acids in the lowered polyunsaturation content in the winter samples suggest selective catabolism of polyunsaturated acids or their transfer to other lipid types and possible *de novo* synthesis of 20:1 and 22:1 fatty acids during the winter. Thus Bute Inlet wax more closely resembles winter samples of *C. plumchrus* than the spring collection.

Calanus plumchrus was common in all zooplankton samples collected in Bute Inlet and was especially dominant in the winter collection. Lipid analyses of other zooplankters from Bute Inlet, including copepods, chaetognaths, ostracods, pteropods, euphausiids, amphipods, decapods, and polychaetes showed that only in the copepod *Gaetanus* sp., *Calanus glacialis* (= *C. marshallae*, according to Frost [1974] and *Heterorhabdus tanneri* did wax ester account for over 15% of the lipid (Lee 1974). These species were minor components of the zooplankton samples except for *Calanus glacialis*, which in the spring accounted for approximately 25% of the zooplankton biomass. The wax ester composition of *Calanus glacialis* is very similar to that of *C. plumchrus* with 20:1 and 22:1 the principal alcohols. Studies by Ackman et al. (1974) have shown similar alcohol composition in copepod species from other areas.

Pristane is a minor component of Bute Inlet wax (Jain et al. 1969). By gas–liquid chromatography we found that 80–90% of the hydrocarbon fraction of *C. plumchrus* was also pristane, in agreement with other work on *Calanus* species (Blumer et al. 1963).

Discussion — We conclude that the origin of Bute Inlet wax is copepod lipid, mainly from *C. plumchrus*. Our supporting evidence is: (1) pristane, the principal hydrocarbon, is well known from marine animals (Blumer et al. 1963; Ackman 1971); (2) Wax esters, the major lipid class present, are also the important lipid of *C. plumchrus*, an important zooplankter in Bute Inlet (Lee 1974); (3) The chain lengths of the wax esters from both sources are similar, as are their alcohol and fatty acid composition and the relative proportions of the various isomeric 20:1 and 22:1 alcohols. The

isomers found in Bute Inlet wax are incompatible with a terrestrial origin; (4) The occurrence of massive kills of zooplankton (R. G. Ackman personal communication; Mohr et al. 1961; Lee and Williams 1974; Cox 1975; Sargent 1976) which our hypothesis requires, and the attribution of a biological origin to natural accumulations of oil in aquatic environments (Banner et al. 1969; Sargent et al. 1977) have been extensively documented (Brongersma-Sanders 1957); (5) Differences between copepod lipids and Bute Inlet wax can be explained by known, but only partially understood, processes of autolysis, autoxidation of the polyunsaturated carbon chains and bacterial degradation (Maxwell et al. 1971).

The specific events leading to the appearance of Bute Inlet wax and the time scale involved are still obscure. Similar material does not occur in the other inlets of this area. Bute Inlet is one of the deepest inlets (650 m) in British Columbia. Glaciers produce a plume of freshwater at its head, and a small stream empties into Bear Bay where the largest amounts of wax collect. We suggest that drastic changes in the physical or chemical character of the water in the Inlet (such as rapid admixture of freshwater from Bear Creek into the seawater in Bear Bay, perhaps induced by strong winds) causes a massive kill of copepods. During the winter the temperature of the upper waters is low enough so that the wax esters solidify and can be washed ashore as solid material. If the kill resulted from freshwater addition it is unlikely to have occurred in the winter, since studies on the life history of *C. plumchrus* have indicated that this copepod is below 150 m in the winter (Fulton 1973).

The wax is less than 300 yr old by carbon-14 dating, according to Williams (1957), but old enough to have lost all polyunsaturated chains. No identifiable zooplankton exoskeletal remains are associated with the wax. We estimate the minimum time scale between living copepods and Bute Inlet wax to be on the order of days to a few weeks, based on published relative rates of autoxidation of monoenoic and polyenoic acids (Holman 1954; Howard and Ingold 1967) and the finding of 16% polyenoic fatty acids in a copepod slick in the North Pacific which at most was a few days old (Lee and Williams 1974).

The occurrence of wax esters in slicks and sediments in many parts of the world's oceans has been well documented. An oil slick in the western Pacific Ocean extended over an area of some 600 square miles. Analysis of the slick showed it to be composed mainly of wax esters with 20:1 and 22:1 the major alcohols (Lee and Williams 1974). Fragments of copepods were recovered from the slick. A slick of wax esters with copepod type structure was reported in the North Sea covering an area of 30 miles (Sargent 1976). Deposits of wax esters frequently wash ashore in certain Norwegian fjords (Sargent et al. 1977). Copepods in these fjords can suddenly be killed when they become trapped in brackish currents. Norwegian fjords are quite similar to Bute Inlet and other fjords in British Columbia. Wax esters containing 20:1 and 22:1 alcohols have also been detected in recent marine sediments collected off the United Kingdom and in diatomaceous ooze from Walvis Bay off southern Africa (Boon et al. 1975; Sargent 1978).

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James Cameron Stevenson

1918-1979

Canada's renowned and respected science editor, James Cameron Stevenson, age 61, died suddenly of a heart attack in Ottawa in the early morning of June 25th, 1979. Cam, as he was affectionately known to his many friends and colleagues, served as Editor of this *Journal* for 17 years, since his appointment in 1962. At his death he was Director and Editor of the Scientific Information and Publications Branch, Department of Fisheries and Oceans, Ottawa.

Cam labored tirelessly and with great effectiveness to build the publications of the Fisheries Research Board of Canada into the most prestigious aquatic science series in the world and in so doing gained well-deserved international recognition for himself and his country.

He was born in Kerrobert, Saskatchewan, on January 16, 1918. After high school, he attended the University of Saskatchewan receiving his B.A. degree in 1939. He was encouraged to study biology by the late Dr. D. S. Rawson. Cam was hired as Limnologist in the university and worked in close association with Dr. Rawson who was establishing a strong limnological centre at the university. In 1942 he received his M.A. degree at the University of Saskatchewan and that same year joined the staff of the Pacific Biological Station, Fisheries Research Board of Canada, at Nanaimo, B.C. His association with the Fisheries Research Board was to be long and fruitful.

Hired as a scientific assistant, he was assigned to work on herring biology and so came under the tutelage of the late Dr. Albert L. Tester. Tester was a fine teacher and a good friend. Indeed, when Cam married Geraldine Gertrude Browne in Nanaimo on July 9th, 1944, the reception was held at the Testers' home and the guests were invited to bring their children — and did. This demonstrated affection for children was a characteristic that Cam would always retain.

Cam was an eager and energetic young biologist and soon had an active research and publication program under way at Nanaimo. He and Tester published a number of joint papers on herring biology but Tester was becoming restless and in 1948 moved to the University of Hawaii. Cam became head of the herring investigation in September 1948 and retained the position until 1953.

He published many papers on the British Columbia herring populations during this period. In 1953 he became scientific assistant to the Director of the Biological Station. It was also during this period that a lasting friendship developed with the late Dr. John L. Hart, and his wife, Olive. John Hart was director of the Pacific Biological Station from 1950 to 1954. Dr. A. W. H. (Alf) Needler became Director in 1954 and Cam became Assistant Director, a position he held until 1959. Alf Needler recalls this period and remembers Cam as a very energetic and involved individual — "a real eager beaver," who had devloped an interest in public relations and communications and took after-hour instruction in these subjects for his own satisfaction.

The Nanaimo years were busy ones. Cam and Gerry's two daughters, Judith Claire and Barbara Kathryn, were born there; in 1950 their house burned down but fortunately most of the contents were saved; and Cam found he had a talent for captivating children by storytelling. His little friends, usually the children of neighbors and associates at the biological station, eagerly sought his company and begged for stories. He was to enjoy thoroughly this relationship throughout his life. He was active in community affairs, particularly the Kinsmens Club and served as President of the Nanaimo branch for a year. He was also President of the British Columbia Natural Resources Council in 1957–58.

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In 1955, having completed residence requirements earlier, he submitted to the University of Toronto his Ph.D. dissertation entitled, "Distribution and survival of herring larvae *Clupea pallasi* Valenciennes, in British Columbia waters" and received his Ph.D. degree. His thesis was subsequently published in the *Journal* in 1962, before he became Editor. This publication was to haunt him in later years. The published account was 75 pages long and included about 20 pages of appendices! As Editor, he was to deplore the publication of wordy graduate theses with long pages of appendix tables, and lectured young biologists on how better to prepare their material for publication.

In May 1959 Cam left the employ of the Fisheries Research Board to become Assistant Director, Pacific Area, Department of Fisheries of Canada, Vancouver, B.C. The position was essentially administrative and provided little scope for his talents.

Then, in 1962, he moved to Ottawa, to become Editor of Publications of the Fisheries Research Board of Canada and Special Assistant (Biology) to the Chairman of the Fisheries Research Board, Dr. Jack Kask. He replaced Dr. W. E. Ricker, who wished to return to Nanaimo. Dr. E. G. Bligh was appointed the new Associate Editor, replacing the late Dr. N. M. Carter, who had retired. Cam moved to Ottawa alone, choosing to find a house for his family before moving them east, which he did within a few weeks.

The staff of the Editor's Office was rather small in those days, just Cam, Graham Bligh, Reg MacIntyre, Dorothy Gailus and Mary Rice. But it was to increase dramatically within the next few years. Cam set about reorganizing his staff and its operations in the offices in the Sir Charles Tupper Building. He was anxious to enlarge the scope of the Board's publications. However, he still had two jobs, Editor and Special Assistant (Biology) to the Chairman of the Board. But in 1965 the Fisheries Research Board decided to support a full-time Editor and Cam was relieved of all other responsibilities. He could now devote full attention to the publication program and soon was delightedly announcing that the *Journal* was to be expanded. In January 1966 it became a monthly publication and soon the Bulletin series would be enlarged as well. Cam's enthusiastic and energetic pursuit of better manuscripts and increased readership became apparent. The growth of the *Journal* alone was phenomenal. For example, an average of 13 articles a year were printed up to 1950, 51 articles between 1950 and 1962, and 224 per year after 1962!

In 1967 the editorial offices were moved from the Sir Charles Tupper Building to the top floor of a small building at 116 Lisgar Street. The next 11 years were to be the most productive and the most professionally satisfying of Cam's career.

He thoroughly enjoyed his work and expressed privately how fortunate he felt to have the perfect job. He was an editor's editor, concerned with policies and procedures, guiding his office and its staff quietly and unobtrusively through turbulent bureaucratic waters, with amazing success. Cam promoted the Board's publication at every opportunity. During scientific meetings or any gathering of fishery scientists he would circulate among the participants finding out what research was being carried out. He would ask scientists visiting from other countries if they knew of the *Journal*, if they subscribed to it, and if not, why not.

For many years he was Secretary to the Canadian Conference for Fisheries Research (and President in 1978–79) and essentially ran the meetings, ably assisted by Mr. John Camp. The annual meetings provided an opportunity for the tall smiling Editor to contact authors, delinquent or otherwise, who had promised a manuscript slated for the *Journal* or perhaps a *Bulletin* — to encourage, cajole, or even, rarely, intimidate them. Many of the Bulletins, for example, resulted solely because of his continuing personal contact with the authors, convincing them of the need to publish the material and data they had in hand or were developing.

Perhaps Cam's greatest strength was his ability to communicate with people — authors, referees, colleagues, and his own staff. He had that rare ability of surrounding himself with exceptionally capable people and inspiring in them a loyalty and devotion that seems rare today. He insisted on high standards for the Board's *Journal* and *Bulletins* but avoided the acrimonious debates that so often develop in such situations. Sometimes his Assistant Editors would travel to a potential "hot spot" and work out, with the author in his own office, difficult portions of manuscripts. At other times, the author would be invited to Cam's office to meet with the Assistant Editor assigned to the manuscript and to resolve difficulties. He was convinced that differences would be resolved if the parties involved could meet face-to-face. Such meetings usually led to lunch of a hamburg and a beer in the basement room of the Lord Elgin hotel, with as many of the editorial staff as were available. Discussions at such times inevitably centered around some aspect of aquatic sciences in Canada.

Meanwhile, the publications issuing from the editorial offices increased many fold and Cam's dream of producing a prime scientific journal of international stature was realized. He was not without critics within the Fisheries branch but nevertheless esteem for the Board's publications was established worldwide. As an editor he had a tremendous handicap for he had very limited sight in one eye. Few people were aware of this, for he never complained.

The preparation of the manuscript on the history of the Fisheries Research Board in which he was deeply involved impressed on him the need for adequate records of events and activities in aquatic sciences in Canada. Hence he undertook to interview in depth a number of former Board members and senior scientists. In all, he recorded on tape more than 20 such interviews in the late 60's and early 70's and deposited this treasury of information in archival storage.

In 1975 Cam Stevenson was installed as the Presi-

dent of the American Fisheries Society, the seventh Canadian to be so honored. He was justifiably proud for it was a demanding role, and he worked diligently during the years of involvement, travelling widely and discharging his responsibilities with care and deliberation.

Cam had few hobbies. A warm, friendly, courteous, and sincere man, he was dedicated to his work and its contact with people. He was a good photographer and on occasion enjoyed organizing a slide show at his home, particularly of his trip to Africa and his and Gerry's trip to Mexico, always providing his inimitable commentary. He loved to garden and for years maintained a small garden on a National Capital Commission plot, enjoying fully the ensuing discussions with neighboring gardeners. A monthly poker game with close friends was a cherished event. But he did not relish retirement, although he tried to prepare himself for it. Those of us who knew him well were saddened by the depression that overtook him during the last few months of his life. But, always the optimist, he had become reconciled to the many changes that were encompassing him.

His colleagues, his staff, and those he loved all miss his smiling soft-spoken gentleness and humility. He fulfilled his dream and left us a tremendous legacy that will endure for all time.

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LETTERS/LETTRES

Comment on "Production, Mortality, and Sustainable Yield of Northwest Atlantic Harp Seals"

Comment

This letter is in response to the article "Production, mortality, and sustainable yield of Northwest Atlantic harp seals (*Pagophilus groenlandicus*)" by G. H. Winters. I wish to comment on four sections: (i) Logistic Changes in Maturation and Fertility Rates, (ii) Surplus Production (Sustainable Yield) of Pups, (iii) Pup Production and Reproductive Stock, and (iv) Maximum Sustainable Yield of Northwest Atlantic Harp Seals. All references to figures, tables, and pages refer to his article unless otherwise specified. The article will be reviewed section-by-section.

Logistic Changes in Maturation and Fertility Rates

The logistic change in mean age of whelping versus population size shown in Fig. 6 is based on three data points. The point having the co-ordinates 2.2 million animals and 6.5 yr is attributed to Sergeant (1966). This point is stated to refer to 1953 by Sergeant. The population size should be the average population from 1948 to 1952 according to the method Winters states, a 5-yr running average with one year lag for year of parturition. The only point in this series given in the cohort analysis (Table 8) is 2.47 million for 1952 and a derivation for this point is not given. Also noting that the population is falling throughout the 1950s, if one were to project back for an average from 1948 to 1952, 2.5 million could be a conservative estimate. Changing the point to 2.5 million from 2.2 million greatly reduces the logistic nature of the data. As hunting greatly decreased during WW II, one would expect minimal population in 1939, with rapid rise after 1944 as new animals become breeders, then falling off as effort increases in the seal hunt. Sergeant (1973) gives a mean age of whelping of 5.6 for the period 1968 to 1971 in the Front which would correspond to a population of 1.3 million using Winters' cohort analysis output averaged from 1963 to 1970. This point does not fall on the curve drawn in Fig. 6. On the basis of the weakness of the 1952 point and the inclusion of the 1968–71 point the data is far less logistic than Winters concludes and may indeed support a linear model, at least locally over the population sizes of the last 25 yr.

Surplus Production (Substainable Yield) of Pups

The surplus production model in this section is based upon the exponential decrease in a year-class,

$$dN/dt = -ZN$$

and a 50:50 sex ratio. By knowing the natural (M) and hunting (F) mortalities and the fertility rate W, the births and deaths may be balanced.

$$(1 - SP)WR = A$$

The notation is as in Winters' except fertility rate is called W to avoid confusion with hunting mortality F, and R is the fraction of females that reach whelping age and SP is the fraction of pups that is surplus production. This was rearranged to give the equation on page 1258. In trying to duplicate the table on the same page the following values were found.

Table 1. Recalculation of Winters' Table on page 1258.

Whelping age (Yr)	R		Surplus production (%)	
	Pup kill only	Universal kill	Pup kill only	Universal kill
4	0.335	0.291	69 (68)	59
5	0.303	0.254	66 (64)	54
6	0.274	0.222	62 (60)	47
7	0.248	0.194	58 (56)	39
8	0.224	0.169	54 (52)	30
10	0.183	0.129	44 (41)	9
12	0.150	0.098	31 (28)	—
13	0.136	0.086	25 (15)	—
14	0.123 (0.120)	0.075	16 (0)	—

Figures in brackets are the values found in Winters'. Surplus production for pup kill only diverges from Winters. This divergence increases with whelping age.

The universal kill surplus production model may be further developed to compare the consistency of the model and the MSY results discussed later. The above equation balancing birth and death rates may be carried ahead further to produce estimates of equilibrium bedlamer and pup catch rates.

$2(1 - SP)R = N_a$ number of seals entering adulthood

$2(1 - SP)RF_A/Z_A =$ adult catch;

$F_A = .015, Z_A = .115$

$(1 - SP)e^{-M} - N_1$ number of one years olds $= X$

$N_1 - N_a =$ number lost in bedlamer phase

$(N_1 - N_a)F_B/Z_B =$ bedlamer catch;

$F_B = .035, Z_B = .135$

All of these rates are in terms of a unit seal born. In order to estimate catch levels it is necessary to have production levels. To do this it was first necessary to relate the whelping ages in the first column of the table on page 1258 to population size. The three points shown in Figure 6 were replotted on semi-log paper as well as the point 3.6 million seals at whelping age 14 mentioned in the second column of page 1259. This semi-log plot was used to interpolate population sizes for each mean age of whelping. A population size of a half million was extrapolated for the The peak total catch is 282 000 with a pup to 1+ ratio of 83:17. It is important to note that these equilibrium yields

whelping age of 4. Once the population sizes were known the equation in Fig. 8 was used to give pup production for each population. With these pup productions and the above formulae for catch level per pup the following estimates were made.

TABLE 2. Sustainable yields using Winters' data and extending his model for universal kill.

Whelping age (Yr)	Approximate population ('000)	Pup prod. ('000)	Pup catch ('000)	Bedlamer catch ('000)	Adult catch ('000)	Total catch ('000)	Pup, 1+ catch ratio
4	500	155	92	5	5	102	90:10
5	1500	398	213	19	12	244	87:13
6	2100	502	235	32	15	282	83:17
7	2350	536	210	44	16	270	78:22
8	2600	564	172	57	17	247	70:30
9	2800	583	119	73	18	210	56:44
10	3000	599	53	91	18	163	33:66
11	3150	608	—	111	19	130	—

are directly dependent upon the pup production. There exists some contradiction between this extended version of the universal kill model on 1258 and the yield curve on 1259 in that they are not compatible because of the varying pup to 1+ ratio in the former.

PUP PRODUCTION AND REPRODUCTIVE STOCK

Winters' model in the previous section incorporates only density-dependent age of whelping with linear age-specific mortality. This is compared to the logistic model form.

$$dN/dt = rN(1 - N/k) - FN$$

where

r = intrinsic growth rate

k = carrying capacity

F = hunting mortality

At equilibrium ($dN/dt = 0$) this leads to the well known Graham-Schaefer surplus yield model.

$$Y_E = F_E N_E = rN_E - (r/k)N_E^2$$

or

$$Y_E/N_E = (r/k)N_E$$

where the subscript E denotes equilibrium.

The model proposed by Winters' in his Fig. 8A is of a similar form, but uses pup production instead of yield, in his notation:

$$P/S = B_0 + B_1 S \qquad B_0 = .66, B_1 = -.000174$$

where P is pup production and S is breeding stock.

This raises two questions: First what does this relationship mean and secondly how were the parameter values, B, determined. As no derivation is cited or given it would appear that Winters, simply picked an arbitrary function to fit his data. It certainly cannot be thought of as an equilibrium curve nor are the data equilibrium points as the population has approximately halved over the period they represent. Therefore, his statement on page 1259 that the peak of this curve is "maximum equilibrium production" is unfounded. Although it is the extrapolated peak production, equilibrium cannot be assumed.

This recruitment relationship can be incorporated into a second order logistic form to yield an equilibrium curve.

The change in population is pupping rate minus death rate.

$$dN/dt = (B_0 + B_1'N)N - MN - FN$$

where B_1' is B_1 adjusted for total 1+ population and M and F are the natural and hunting mortality rates. $B_1' = B_1/2$ with 50:50 sex ratio.

In equilibrium we find

$$FN_E = (B_0 + B_1 N_E)N_E - MN_E$$

With no hunting mortality the aboriginal stock size from such a model is

$$N_E = (B_0 - M)/B_1$$

The equilibrium yield is the difference between the birth and natural death rates. If a 50:50 sex ratio and Winters B_0 and B_1 are assumed, the aboriginal population is $(0.66 = 0.1) \div 0.000087 = 6.4$ million, as opposed to Winters estimate of 3.6 million. Winters asserts that the peak of his production curve represents the aboriginal stock size. This is not consistent with an equilibrium model in general, or a Graham-Schaefer in particular, as it does not balance the birth rate against a death rate.

The above discussion has assumed Winters' value of B_0 and B_1, but in attempting to reproduce these regression coefficients it was not clear how the reproductive stock was defined; was geometric mean or Y on X (predictive) regression used; or if the data were smoothed by some unreported technique. In order to try and answer these questions a number of regressions using Winters' data were carried out with the following results.

	Pups	Female 1+ pop.	5-yr. avg.	Regression	r	B_0	B_1	Peak pop. ('000)	Pup prod. ('000)
1	Cohort	50:50	—	*Y on X*	0.68	0.673	−0.000185	1818	612
				GM		0.733	−0.000272	1364	506
2	Cohort	50:50	*S*	*Y on X*	0.72	0.621	−0.000208	1614	542
				GM		0.732	−0.000287	1276	467
3	Cohort	50:50	*P, S*	*Y on X*	0.82	0.675	−0.000185	1826	617
				GM		0.707	−0.000216	1566	554
4	S.I.[a] + Proj.	50:50	*S*	*Y on X*	0.92	0.721	−0.00291	1238	447
				GM		0.742	−0.000318	1166	433
5	S.I. + Proj.[b]		*S*	*Y on X*	0.90	0.690	−0.000259	1331	459
				GM		0.712	−0.000288	1238	441

[a]Pup data from Winters' Tables 1 using GM regression and Table 6.
[b]Female population is average 50:50 and sex ratios in Winters' Table 3.

Because of the large uncertainty in both pup production and population size the GM regression is indicated. The geometric mean regression markedly lowers the estimates of peak population and maximum pup production. In the first three pair of regressions the pup productions from the cohort analysis were used. The first pair used unsmoothed data, the second pair 5-yr averaged S (Winters' reproductive stock) and the third 5-yr averaged both P (pup production) and S. The Y on X regression in this third pair most closely resembles the r, B_0, and B_1 given by Winters. This resemblance, the observation that only 20 of the 27 data are plotted in Fig. 8A and the failure I had in reproducing Winters results suggest that an unspecified method of data smoothing was used.

The significant improvement in correlation when the pup data used are derived from the survivorship index results combined with Winters projection from 1973 to 1978 is accompanied by a reduction in peak production and population size. Refining the estimate of the female population size produced only a minor shift, as is seen when the fourth and fifth pair of results are compared.

The GM regression with lagged stock size and the GM regression for the survivorship index data indicate a peak production between 440 and 470 thousand. The regression which used smoothing on both P and S biases the correlation coefficient upwards and is weaker than an r of 0.82 implies. These results suggest that the 615 000 peak pup production which Winters used is quite optimistic. This difference is very important as the pup production is the foundation of the sustainable yield calculation.

Maximum Sustainable Yield of Northwest Atlantic Harp Seals

The method used to produce Fig. 9 is very briefly given. It is interesting to directly use the given pup catch and population size (Tables 1 and 8) to form an estimate of MSY. Using a GM regression between pup catch over 1+ population versus 1+ population gave an MSY pup estimate of 206 000 which should be increased by 25% to incorporate an 80:20 catch ratio of 0:1+ this yields an MSY estimate of 258 000 at a population of 1.46 million. When the population was lag averaged over 5 yr the MSY estimate was 248 000 at a population of 1.45 million. When the data were analysed using the method of Schnute (1977) the coefficient of determination was 2.5% showing that the data are poorly fitted by the logistic model.

The third paragraph proposes a deceptively simple method of estimating sustainable yield by looking at the change in population size over a 20-yr period and subtracting this from the averaged catch. To test this approach the model published in Lett and Benjaminsen (1977) was used with an arbitrary stable starting 1+ population of 2.78 million. With an 80:20 catch ratio, the MSY for this model is near 240 000. The following populations resulted with a catch 65 000 greater than MSY.

Year	1+ Pop. (10^6)	Change/Yr. ('000)	Catch ('000)	'MSY' est. ('000)
0	2.78			
10	2.47	31	315	284
20	2.19	28	315	287
30	1.93	26	315	289
40	1.66	27	315	288
50	1.34	32	315	283
Average		29		286

The estimates formed by the method proposed by Winters are in considerable error to 240 000, the modeled stock MSY. The reason for this is that males and to a lesser extent immature females have a reduced reproductive value. So although the catch was 65 000 above MSY, less than half of this "excess" catch effected the pup production of the herd. This demonstration uses the Lett and Benjaminsen model which assumedly possesses similar dynamics to the seal herd.

If a logistic model is assumed, and the stock harvested from the virgin state at a rate in excess of MSY, the change in population size would be greatest at the point furthest from the MSY population size. This point is made by Winters in the last paragraph on page 1259 and is the basis for calling his a minimum estimate. So, on one hand we have the reduced reproductive value of males and immatures causing this method to overestimate. On the other, we have a degree of underestimation caused by an unknown amount of reduction in the sustainable yield depending on popula-

tion size. These opposing effects are large, difficult to estimate, and therefore, greatly reduce the value of the resultant MSY.

The modeled 50-yr population decrease contradicts the last method presented on page 1259, that of using the long-term kill. The long-term average in a collapsing population is no indication of its MSY, viz. 315 vs. 240 thousands. The difficulty with these two methods is that they are trying to directly apply an equilibrium concept, sustainability, to data from a nonequilibrium stock. Another ramification of sustainability is an implied constant carrying capacity. Environmental change, especially in terms of fish stock abundance may have significantly changed the carrying capacity during the last century and a half. In the case at hand of the, until recently collapsing harp seal stock, neither of the methods brought forward in the last paragraph of 1259 are applicable with confidence.

To recapitulate, the logistic mean age of whelping function was shown to be weak due to an unsubstantiated point and a point overlooked in the literature. The data on the relationship between whelping age and population size does not show a clear trend and one would be hesitant in fitting a linear let alone a higher order function through them. Winters subsequently used the logistic in Fig. 6 to develop surplus yield of pups and maximum sustainable yield estimates. The surplus production results given on page 1258 contained errors which were probably carried on into his MSY estimates. The surplus production model under universal kill in conjunction with his pup production function was developed further than by Winters to produce a sustainable yield table (My Table 2). This table does not agree with the yield curve shown two sections larger on page 1259.

The pup production section was seen to be error ridden. Winters states on pages 1258–1259, "The Graham-Schaefer type curve thus derived indicates a maximum equilibrium production of 615 000 animals occurring at a population size of 1.8 million 1+ females equivalent to a total 1+ population of 3.6 million animals which is an estimate of the aboriginal population level of Northwest Atlantic harp seals." As his pup production is not an equilibrium model it is not Graham-Schaefer; the maximum of Fig. 8B is not the maximum equilibrium production and the aboriginal stock size is incorrectly derived. As well as the theoretical basis for this section being quite weak the regression coefficients could not be reproduced. Instead lower peak pup production were indicated by the data derived earlier in his paper.

The maximum sustainable yield section produces estimates of MSY based upon pup production and upon historical catch levels. By using coefficients derived in this letter the MSY and MSY population fell much closer to other published estimates. The historical catch data is from a nonequilibrium stock and the method was shown to be susceptible to large errors. It is concluded that because of the lack of theoretical basis, especially the concept of equilibrium, a complete reworking of this data is needed.

Due to the considerable length this letter has already reached, I will not comment on the rest of the sections. Perhaps the difficulties I had reproducing and understanding Winters' findings are due to my inability to follow sound arguments. If this is so my apologies are extended to the author. On the other hand, as the public has a high interest in the harp seal herd and its management, it is of particular importance that articles published pertaining to this question be lucid and accurate. — ROBERT K. MOHN, *Marine Resources Analysis Limited, P.O. Box 527, Dartmouth, N.S. B2Y 3Y8.*

LETT, P. F., AND T. BENJAMINSEN. 1977. A stochastic model for the management of the northwestern Atlantic harp seal (*Pagophilus groenlandicus*) population. J. Fish. Res. Board Canada. 34: 1155–1187.

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REPLY

The above letter by Dr R. Mohn re my harp seal paper (JFRBC 35: 1249–1261) contains many inaccurate comments which are both a result of misunderstanding of the analytical techniques used (due mainly to my inadequate description of these techniques) and a poor familiarity of the harp seal data base by Dr Mohn. I will, therefore, restrict my reply to those comments of Dr Mohn's which are either based on a misinterpretation of the data and/or my analyses of such data, or which imply an internal inconsistency in my paper.

A. LOGISTIC CHANGES SECTION

1) The maturation data used were collected during 1951–54 by both Sergeant and Fisher (Sergeant 1966). I selected 1952 as the midyear and thus if 1951 is the year of parturition the 5-yr running average for the 1952 point in my Fig. 6 refers to the average 1+ population size for the years 1946–50. Interpolation from Ricker (1971) suggested that the population level of harp seals in the late 1940s was about 90% of the level in the early 1950s. This was further substantiated from back-calculation of the strengths of the 1946–50 year-classes from my age-specific cohorts for 1952 (Table 8) assuming a similar age-specific catch distribution as in 1952. The average strength of these year-classes was 500 000 animals or roughly 90% of the 1952 level. The 1+ population for the late 1940s was, therefore, calculated to be $2470 \times 10^{-3} \times 0.90 = 2220 \times 10^{-3}$ animals which is the value shown in Fig. 6.

2) Dr Mohn has obviously not seen the basic data on which the mean whelping age of 5.6 yr (Sergeant 1973) is based. An examination of this data (given in Sergeant 1976) led me to discard this estimate as being statistically worthless since it was based on a total sample size of eight individuals in the main critical ages (4 and 5-yr-olds).

3) Given the poor sampling data and inaccurate catch

statistics for the 1950s any estimate of population size during that period must be considered very approximate although biologically a linear relationship between population size and maturation rate would not be expected.

B. Surplus Production of Pups

1) Table 1, Col. 4 is indeed in error and Dr Mohn's values are the correct ones.

2) The yield curve in Fig. 9 is not based on the particular parameters used in the universal kill model on p. 1258 which is shown for illustrative purposes only. Lines 6–9 (p. 1259, right-hand column) describe the basis for the parameters used in Fig. 9. They are the average 1975-77 fishing mortality rates exerted on the bedlamers ($F = 0.040$), adult females ($F = 0.011$) and the 1+ population ($F = 0.032$). The calculations are correctly executed and indicate an MSY of 290 000 animals of which 80% are pups. Since maintaining the same F values (rather than a constant pup/1+ ratio) implies a varying Pup/1+ ratio I felt no need to expound the axiom.

C. Pup Production and Reproductive Stock

1) An inadequate description of my analytical methodology in this section has resulted in some misinterpretation of my results by Dr Mohn. To approximate equilibrium conditions I have used the conventional Gulland modification of the Grahamn-Shaefer model (a 5-yr running average, equivalent to the mean exploited life-span). To avoid the unrealistic fluctuations in pup production from year-to-year evident in cohort analyses I have averaged the pup strength of a particular cohort with its two adjacent cohorts.

2) Since the production curve in Fig. 8A was intended as a prediction of pup strengths the predictive equation (Y on X) was naturally used.

3) Since historical catch statistics indicate a substantial number of annual kills exceeding 500 000 animals (up to a maximum kill of about 650 000) I do not feel my peak production of 615 000 pups to be at all optimistic but these historical kills instead suggest that the estimates from the GM regression (440 000–470 000) are indeed very pessimistic.

4) I have assumed in Fig. 8B that nobody would seriously interpret the right-hand descending line as representing the stock–recruit relationship in such a nondynamic stock as harp seals and the model was presented merely to calculate pup production up to maximum levels. Since the available data suggest a lower whelping limit of 4 yr the reproductive stock should really be defined as 4+ females rather than 1+ females as I did, merely as a convenience in calculation of surplus yields in Fig. 9. Utilizing 4+ females would undoubtedly result in a nonlinear relationship between P/S and S (see Winters 1976) which would produce a Beverton-Holt type stock–recruit curve as one would expect for a harp seal population.

D. MSY Level

1) The simple method used by Mohn (Pup catch/1+ population size ratio) to estimate MSY is rather approximate in that it does not take into account the sex ratio of the adult kill, nor the proportion of bedlamers to adults. Nevertheless his calculations are in error due to (a) the actual 0: 1+ ratio being 74.5% rather than 80% — this increases Mohn's MSY estimate from 258 000 to 278 000 animals in the case of the unsmoothed data and from 248 000 to 266 000 in the smoothed case. (b) Mohn's method assumes that pup exploitation rates are inversely related to population size ie. as the population declined increased hunting effort was expended to maintain pup kills at high levels. This assumption does not hold true after the introduction of quotas in 1972 when hunting effort was controlled by regulation. Thus recalculating the data up to 1971 results in an MSY estimate of 335 000 animals at a population size of 1.7 million (the coefficient of determination increases to 37%).

2) On p. 1259, third paragraph of my paper I utilize a method which Mohn describes as a "deceptively simple" one to arrive at a minimum estimate of MSY under kill conditions as they existed during the early 1950s and 1960s (0:1+ kill of 70%, $1+ F = 0.050$). This is considered to be a minimum estimate since the population was increasing during the late 1940s and early 1950s and was above the estimated MSY level in 1952 when the forward projections were done. Since Mohn implies that this method is not valid I present below the calculations on which the statement was made (the parameter values used are those given in my paper and $C_t^1 = C_t - 70\,000$, distributed according to the 0:1+ ratio for year t).

Year	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
Pup. prod. ($\times 10^{-3}$)	551	560	548	535	520	516	510	496	494	492	500
1+ Pop. ($\times 10^{-3}$)	2470	2490	2540	2510	2450	2340	2370	2320	2270	2300	2410
	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	
Pup. prod. ($\times 10^{-3}$)	500	500	510	525	545	565	585	587	610	625	
1+ Pop. ($\times 10^{-3}$)	2400	2360	2330	2420	2450	2480	2610	2710	2810	2940	

Since Lett et al. (1978) have substantially discarded many of the calculations on which the Lett and Benjaminsen (1977) model was based and since most of its parameter functions have been cast in doubt (see Anon. 1979) I wonder why Mohn has gone through his exercise at all.

The long-term kill may be considered an estimate of MSY providing (a) the stock has not been under continuous decline during the period, (b) sufficient generations have been subjected to exploitation, (c) environmental conditions have remained relatively constant. From historical catch statistics and such sources as Chafe (1923), Colman (1937) and more recent analyses it is evident that the harp seal population declined during the 1800s, recovered during the period 1914–24, probably stabilized during the period 1925–38, increased during 1940s up to the early 1950s and then declined to the early 1970s. Insofar as condition (b) is

concerned the mean Z for the recent period (1952–78) is 0.25 (all age-groups). Taking a conservative level of 0.20 for the entire historical period of 150 years implies 30 generations which, if the population were in continuous decline would suggest extinction of the herd 30–40 yr ago. With regard to environmental conditions there is no hard data to suggest a dramatic change in the environment over the past 150 yr nor can we predict major environmental conditions in the near future. Thus the long-term average kill can be taken as a minimum estimate of MSY and since it does not rely on tenuous sampling data for evaluation of M, fertility or whelping rates it is probably our best estimate of harp seal productivity.

I trust that the comments contained in my reply to Dr Mohn's critique of my paper elucidate many of the points which he has raised and have clarified any misunderstandings. I apologize to your readers for not providing a detailed description of some of the analytical procedures involved and extend this apology on behalf of the reviewers of my paper who obviously felt that concision did not significantly detract from the understanding of the analyses. — GEORGE H. WINTERS, *P.O. Box 5667, St. John's, Nfld. A1C 5X1.*

ANON. 1979. Report of Standing Committee on Research and Statistics (STACRES) — Special Meeting on Seals and Shrimp, November 1978. ICNAF Sum. Doc. 79/VI/I, Ser. no. 5317.

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LETT, P. F., R. K. MOHN, AND D. F. GARY. Density-dependent processes and management strategy for the Northwestern Harp Seal. ICNAF Res. Doc. 78/XI/84, Ser. no. 5299.

RICKER, W. E. 1971. Comments on the West Atlantic Harp Seal herd and proposals for the 1972 harvest. ICNAF Res. Doc. 75/XII/143. (Appendix).

SERGEANT, D. E. 1973. Environment and Reproduction in seals. J. Reprod. Fertil. (Suppl.) 19: 555–561.

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WINTERS, G. H. 1976. Estimation of mortality rates and surplus production of Northwest Atlantic harp seals. ICNAF Res. Doc. 76/X/127. Ser. no. 4014.

1978. Production, mortality and sustainable yield of Northwest Atlantic harp seals (*Pagophilus groenlandicus*). J. Fish. Res. Board Can. 35: 1249–1261.

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BOOK REVIEWS/COMPTES RENDUS

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Salmon and Trout Farming in Norway. *D. J. Edwards. Fishing News Books, Ltd., Farnham, Surrey, England. 1978. 195 p. £9.00.*

The production of 2–k kg cultured Atlantic salmon and rainbow trout in Norway has grown from 150 t in 1971 to over 4500 t in 1978.

The success of the industry is based on: a well-protected coastline with numerous sites for farms; waters from the Gulf Stream which are close to ideal for salmon, 5–18°C; large quantities of suitable food from the commercial fishing industry; a supply of skilled labor in the commercial fishing industry; techniques from the commercial fishing industry, such as holding fish in cages and live transportation of fish, which could be adapted to fish culture; good biological and technical research and development. In "Salmon and Trout Farming in Norway" Dr Edwards discusses the early development of the industry, production cycles, freshwater rearing techniques, siting of saltwater farms, fixed sea units, floating net cage techniques, feeding, disease, marketing, economics, and future requirements and trends of this rapidly growing industry.

While I was already aware of the success of the industry and familiar with the very good research studies coming from the group with which Dr Edwards was associated, the technical practicalities described in the book added much to my understanding of the salmon and trout farming operations. The physical similarities between the Norwegian coastline and the west coast of North America mean that this publication will be of particular interest to those active in cage culture of Pacific salmon. The generalities will be of interest to cage culturists throughout the world.

The book is well organized and abundantly illustrated. The only typographical errors I noticed were the failure to provide a legend for the photograph on page 92 and the incorrect use of "1 mμ" rather than "1 μm" on page 23. One statement which caught my attention was, "Salmonids require a high level of dissolved oxygen in the water, and therefore do not tolerate a high temperature" (page 3). The implied relationship escapes me. At 24–25°C, the lethal temperature for salmon, 100% saturation is 8–9 mg/L of dissolved oxygen which is well above the 5–6 mg/L dissolved oxygen necessary for good growth. Another, on page 10, suggests that salmon "home" by detecting chemical substances, pheromones, released by other fish. This is a very tentative hypothesis. In general, however, I found the factual content of the book to be very good.

One interesting aspect that may or may not be affecting the industry is that the Norwegian government treats aquaculture as a vehicle for rural development and has restricted the size of individual farms to a production capacity of 8000 m^3. This means production is distributed over many small units and the benefits of the industry are spread as much as possible. This does not seem to be the case in North America.

Dr Edwards' writing is lucid and easy to read.

I would not hesitate to recommend this book. It is a welcome addition to its publisher's fine list of publications on aquaculture.

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(R236)

Chemical Modelling in Aqueous Systems. Speciation, Sorption, Solubility, and Kinetics. *Edited by Everett A. Jenne. ACS Symposium Series, American Chemical Society, Washington, D.C. 1979. xii + 914 p. $59.50.*

This book, nearly 900 pages of varied subject matter that was presented at the American Chemical Society's 1978 Symposium, is a collection of 37 technical papers by 97 authors. The papers fall into six broad categories: redox processes, organic ligands, adsorption processes, evaluation and estimation of thermodynamic and kinetic data, interfacing with biological models, and comprehensive models and applications. There is, of course, considerable overlap between these categories; in addition, the papers are for the most part a hybrid between a review and a data-information paper. Much of the data presented is not new, but the limitation imposed on contributors was simply that ". . . verbatim reproductions of previously published papers are not accepted." The strength of this book is in the expert review and discussion of the subject matter. While specialists may not find dramatically new revelations in their particular areas of interest, they will undoubtedly find many ancillary topics that will broaden their horizons. Those with sufficient fortitude to read the entire volume will be brought up to date on nearly the entire front of physical chemistry of natural aquatic systems.

The treatment of redox processes is comparatively brief (three papers) which is disproportionate to their importance in natural systems. Platinum electrode potentials were once measured frequently in natural systems, but the value of these measurements was much deprecated in the past by purists. Two papers in this section present a welcome clarification of such measurements in terms of the chemistry of sulfur and iron. Less enlightening is the third paper on the electrochemistry of arsenic, a purely applied study.

The "organic ligands" section contains an elegant and concise paper on determination of acidity constants of humic acid by the thermochemical titration method. In two other papers, the redetermination by the ion exchange method of the copper-humic acid stability constants, and the ion exchange constants for alkali and alkaline earth ions with hydrogen ion on humic acid are presented. In both cases the humic acid in solution is regarded strictly as a solid ion exchanger without regard for the concomitant ionization processes in solution that are not driven by ion exchange. This is puzzling in the absence of any stated reasons for this approach. In the area of humic substances research, it is frequently difficult or impossible to extract from published works unambiguous constants that can

readily be used for predictive purposes. The same difficulties are encountered here to some extent. A new and lower stability constant for the dihydroxy copper complex is presented in another paper. This should be of interest to anyone concerned with the calculation of chemical species. The redetermination is based on measurements with the cupric ion-selective electrode, assumed to be insensitive to inorganic cationic complexes of copper, which may not be true. In view of this uncertainty, the accuracy of this new constant is also in doubt for the time being. The paper on complexing of nickel by microbial metabolites will be of interest to microbiologists and chemists alike, and the concept of a stability function as presented in the final paper of this section should prove to be a very useful tool in modelling of aquatic systems.

The papers presented in the "adsorption" section exemplify well the difficulties that this area of research presents. When investigating adsorption by natural sediments in the laboratory, a particular sediment representing some aquatic system is used, which necessarily makes each such experiment specific. These experiments would therefore not be expected to yield generally predictive results. The incorporation of adsorption processes in a generalized way into chemical speciation models will be difficult but apparently not impossible if these papers are any indication.

The existing deficiency in knowledge of thermodynamic and kinetic constants is the bane of modellers of aquatic systems. Significantly, the section on "evaluation and estimation of thermodynamic and kinetic data" is the largest section in terms of numbers of papers. Some papers here deal with rather narrow subjects such as formation of the mercury-containing minerals schuetteite and corderite under oxidizing and highly acidic conditions, the free energies of formation of sepolite and kaolinite, the kinetics of calcium phosphate formation, and a brief but concise review of the aqueous chemistry of plutonium, timely in view of the notoriety of this element. A very extensive exposition of the various correlations of physico-chemical data of some elements, and techniques of estimating thermodynamic constants from a limited data base are presented in another paper. Despite the apparently "good" constants that some of these techniques can yield, they are methods of last resort. There is no hint here that the production of much needed constants is under way by more direct means. The precipitation and dissolution of calcium carbonate and silicates are given much attention (two papers each), appropriate in view of the commonplace occurrence and importance in nature of these processes. The exclusion (except for some passing references) of the subject of metastability from this volume is regrettable. The scope of the book is obviously not restricted to equilibrium systems; the omission of any discussion or review of metastability as it pertains to natural systems will not, it is hoped, encourage unrealistic modelling approaches.

Only four papers make up the section on "interfacing with biological models." These four papers are, however, extensive and ambitious in scope, ranging from the purely experimental to the theoretical. The experimental papers suffer somewhat from lack of experimental rigor and definition. The experimental results and their subsequent interpretations are heavily dependent on operational steps in the procedures, which diminishes their absolute value, although their pedagogic value is still considerable. An excellent paper on application of factor analysis to chemical speciation in toxicology shows well the dangers of venturing into the toxic-species mine-field without the appropriate statistical accoutrements.

An increasingly large number of computer programs are being used to calculate concentrations of chemical species in natural waters and other complex aqueous media. The question of consistency of results obtained by using different programs has naturally arisen. An answer to this question is given in a paper in the section on "comprehensive models and applications." Thirty computer programs were surveyed, and thirteen of these were examined more closely for consistency in terms of the calculated log of concentration of various chemical species. Two of the larger programs are further discussed in two separate papers, largely with respect to their evolution. The remaining six papers in this section should be of interest to chemical oceanographers, limnologists, and physical chemists.

Science libraries should certainly have this volume on their shelves. Research managers would very probably benefit from a perusal of the introductory paper in the book, which focuses on managerial aspects of research and contains a very readable epistle on the interdisciplinary approach to research.

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(R263)

Books Received/Livres reçus[1]

June/juin–July/juillet 1979

***Fourth National Workshop on Entrainment and Impingement.** *Edited by Loren D. Jensen. E A Communications Division of Ecological Analysts, Inc., Melville, N.Y. 1979. xx + 424 p. $14.95.* (Proceedings of the Workshop held in Chicago in December, 1977. Includes sections on Regulatory Issues, Impingement Studies, Impact Assessment Techniques, and Engineering Aspects of Entrainment and Impingement.)

***Atlas of British Columbia.** *A. L. Farley. University of British Columbia Press, Vancouver, B.C. 1979. viii + 136 p. $45.00.* (A beautifully prepared atlas of B.C., but contains little of interest to fisheries scientists.)

***Marine Biology.** *John Reseck. Prentice-Hall, Inc., Englewood Cliffs, N.J. ix + 257 p. $16.50.* (Although well printed and illustrated, this book is approximately at the level of first year university general science.)

Principles of Warmwater Aquaculture. *Robert R. Stickney. John Wiley & Sons, Inc., Somerset, N.J. 1979. xii + 375 p. $22.50.* (An introductory text on many aspects of aquaculture of warmwater organisms, including extensive literature citations, and suggested additional reading.)

Fisheries ecology of floodplain rivers. *Robin L. Welcomme. Longman Group Ltd., London, England. 1979. viii + 317 p. $64.85.* (A small, highly packed book covering many aspects of floodplain river ecology, but at a very high price.)

***Phytoplankton manual.** *Edited by A. Sournia. UNESCO Series, Paris, France. xvi + 337 p. ?* (One of the UNESCO series on quantitative biology.)

***Fish and Invertebrate Culture. Water Management in Closed Systems.** *2nd ed. Stephen Spotte. John Wiley & Sons, Inc., Somerset, N.J. 1979. xvi + 179 p. $13.95.* (This book is almost entirely devoted to aquacultural engineering of water systems.)

Marine Pollution: Functional Responses. *Edited by Winona B. Vernberg, Frederick P. Thurberg, Anthony Calabrese, and F. John Vernberg. Academic Press, Inc., N.Y. xiii + 454 p. $23.00.* (Proceedings of the Symposium "Pollution and Physiology of Marine Organisms" held on November 14–17, 1977 in Georgetown, South Carolina.)

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[1]Entries in this list *not* marked by an asterisk are available for review by interested readers for a 3-month period from the time of publication of the list. For information, please write to the Book Review editor.

[2]Les ouvrages inclus dans cette liste et *non* accompagnés d'un astérisque peuvent être mis à la disposition de lecteurs intéressés qui voudraient en faire l'analyse, et ce, pour une période de 3 mois à compter de la date de parution de la liste. Pour plus de renseignements, veuillez écrire au rédacteur des Comptes rendus.

ANNOUNCEMENTS/AVIS

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An author–subject index and list of all publications issued during 1979 will be supplied in early 1980, and distributed free to all *Journal* recipients, including subscribers. Additional copies will be available through the Scientific Information and Publications Branch.

Index

Un index par sujet et auteur et une liste de toutes les publications parues en 1979 paraîtront au début de 1980 et seront distribués gratuitement à tous ceux qui reçoivent le *Journal,* ainsi qu'aux abonnés. On pourra se procurer des exemplaires supplémentaires à la Direction de l'information et des publications scientifiques.

Subscriptions

Subscription rates effective January 1980 are $47.00 per year in Canada and $56.40 per year in other countries. Single issues are $4.00 and $4.80, respectively.

The subscription rate for the *Journal* has not been increased over the past two years. During this period printing and associated costs, distribution and postal rates, have increased by 30%. We regret therefore, that the subscription price for 1980 must be increased by 17% to recover those costs that cannot be absorbed in any other way. If at all possible, we will avoid a further increase for 1981.

Abonnement

À compter de janvier 1980 les frais d'abonnement annuel seront de $47.00 pour le Canada et de $56.40 pour les autres pays. Chaque numéro coûtera $4.00 au Canada et $4.80 à l'étranger.

Le prix de l'abonnement au *Journal* n'a pas augmenté depuis deux ans. Pendant cette période, les coûts d'impression et autres, les frais de distribution et les tarifs postaux ont pourtant connu une hausse de 30%. Nous sommes donc au regret d'avoir à augmenter de 17% le prix de l'abonnement en 1980 pour couvrir les coûts que nous ne pouvons pas absorber autrement. Autant que possible, nous éviterons d'augmenter les tarifs de 1981.

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

New and rare records of Canadian fishes and the influence of hydrography on resident and nonresident Scotian Shelf ichthyofauna **D. F. Markle, W. B. Scott, and A. C. Kohler**

Terebellidae (Polychaeta) from the Northeast Pacific Ocean **K. Banse**

Production of nonviable oocytes by Pacific hake (*Merluccius productus*) **R. P. Foucher and R. J. Beamish**

Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York **L. A. Nielsen**

Association and feeding relationships between *Eogammarus confervicolus* (Amphipoda, Gammaridae) and benthic algae on Sturgeon and Roberts Banks, Fraser River Estuary **W. M. Pomeroy and C. D. Levings**

Oxygen depletion in Lake Erie: Has there been any change? **M. N. Charlton**

Simulations of energy flow through the amictic female rotifer *Brachionus rubens* Ehrbg. **J. Majkowski, J. Pilarska, and R. Z. Klekowski**

Séparation des populations de hareng de l'Atlantique (*Clupea harengus harengus*) de l'estuaire du Saint-Laurent et de la péninsule gaspésienne **G. Côté, P. Lamoureux, J. Boulva et G. Lacroix**

Role of gut flora in the transfer of amino acids through a marine food chain **W. Fong and K. H. Mann**

Genetic changes in hatchery stocks of brown trout (*Salmo trutta*) **N. Ryman and G. Ståhl**

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A simple reflectance method for the measurement of particulate pigment in lake water and its application to phosphorus–chlorophyll–seston relationships **M. Bergmann and R. H. Peters**

Interspecific predation of common Strait of Georgia planktonic coelenterates: laboratory evidence **M. N. Arai and J. R. Jacobs**

Concentrations of leucine aminonaphthylamidase (LAN) and soluble protein in tissues of rainbow trout, *Salmo gairdneri* **G. R. Bouck**

Analysis of double-tagging experiments: an update **H. J. Russell Jr.**

Leaf litter processing in a regulated Rocky Mountain stream **R. A. Short and J. V. Ward**

A motion for the retirement of the von Bertalanffy function **D. Roff**

Perspectives

The river continuum concept **R. L. Vannote, G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing**

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Volume 36, No. 12, December 1979 Volume 36, nº 12, décembre 1979

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